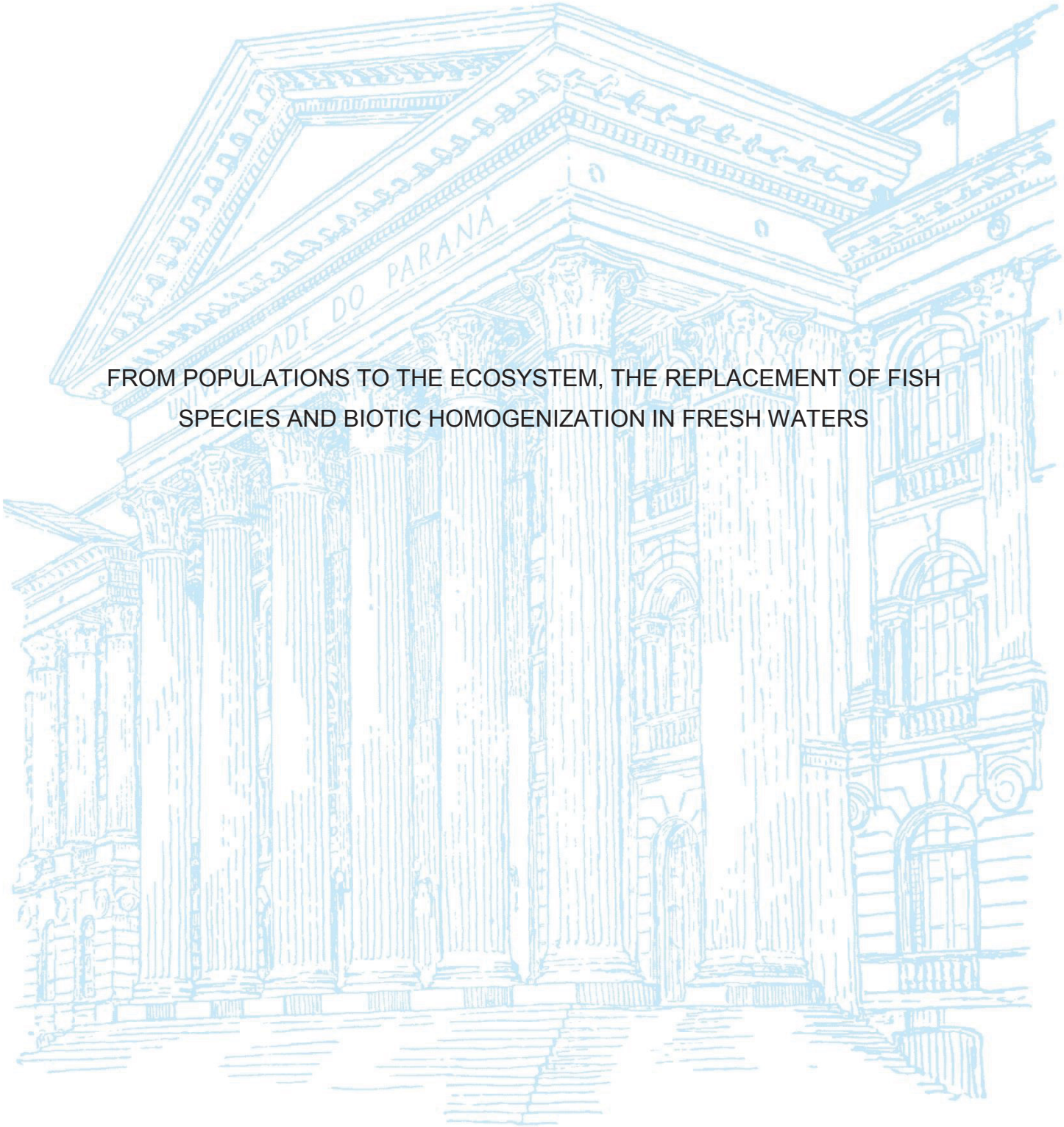
UNIVERSIDADE FEDERAL DO PARANÁ

LUIS ARTUR VALÕES BEZERRA



FROM POPULATIONS TO THE ECOSYSTEM, THE REPLACEMENT OF FISH SPECIES AND BIOTIC HOMOGENIZATION IN FRESH WATERS

CURITIBA

2019

LUIS ARTUR VALÕES BEZERRA

FROM POPULATIONS TO THE ECOSYSTEM, THE REPLACEMENT OF FISH SPECIES AND BIOTIC HOMOGENIZATION IN FRESH WATERS

Tese apresentada como pré-requisito parcial para obtenção do título de Doutor em Ecologia e Conservação pelo Programa de Pós-Graduação em Ecologia e Conservação da Universidade Federal do Paraná (PPGECO, UFPR), Setor de Ciências Biológicas.

Orientador: Dr. André Andrian Padial
Coorientador: Dr. Simone Libralato

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TERMO DE APROVAÇÃO

Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação em ECOLOGIA E CONSERVAÇÃO da Universidade Federal do Paraná foram convocados para realizar a arguição da Tese de Doutorado de **LUIS ARTUR VALÕES BEZERRA**, intitulada: **FROM POPULATIONS TO THE ECOSYSTEM, THE REPLACEMENT OF FISH SPECIES AND BIOTIC HOMOGENIZATION IN FRESH WATERS**, após terem inquirido o aluno e realizado a avaliação do trabalho, são de parecer pela sua Aprovação no rito de defesa.
A outorga do título de Doutor está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

Curitiba, 08 de Maio de 2019.

ANDRE ANDRIAN PADIAL
Presidente da Banca Examinadora

RONALDO ANGELINI
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Avaliador Externo (UEM)

To my family and to all those who made it possible.

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“Nada es tan desalentador como un esclavo satisfecho”

Ricardo Flores Magón

“…Organisms not only adapt but they also change the environment…”

Eugene Pleasants Odum

RESUMO

Enquanto você está lendo este resumo, barramentos e a introdução de peixes não-nativos ameaçam a biodiversidade global e causam a perda de espécies e grupos funcionais em ambientes aquáticos. Mesmo em ecossistemas altamente diversificados, como várzeas neotropicais, o aumento no número de espécies introduzidas não implica em maior biodiversidade. Invasões biológicas, dominação por espécies de fundo ("benthification"), oligotrofização e "trophic downgrading" são processos chave que ameaçam a biodiversidade de peixes. Comparamos a abundância de peixes que se alimentam no fundo com pelágicos e predadores de topo em ecossistemas dulcícolas (lagos e reservatórios), em nível global. Além disso, combinamos 18 anos (2000-2017) de capturas, por redes de espera e arrastos, de peixes, organizados em grupos funcionais, na planície de inundação do alto rio Paraná, para descrever como a homogeneização biótica está moldando a biodiversidade, mesmo com a manutenção do número de espécies. Demonstramos um agrupamento de espécies nativas em poucos grupos funcionais, também influenciado por espécies não-nativas. Isso gerou redundância em várias métricas de biodiversidade, como biomassa, tamanho, densidade e interações de redes alimentares. Os padrões encontrados refletem os efeitos de bento-pelágicos e demersais, no processo de dominância por predadores de fundo, além da dominância em níveis tróficos intermediários (a liberação de “meso-predators”) e o sucesso de indivíduos não-nativos. Poucos grupos substituem muitos grupos funcionais e perturbam os ecossistemas de forma muito previsível, causando a perda de espécies raras e biodiversidade. Consequências imediatas da homogeneização biótica é o colapso da atividade pesqueira, a perda da qualidade da água e o desaparecimento de serviços ecossistêmicos cruciais (por exemplo, controle de pragas, ciclagem de nutrientes e dispersão de plantas). O desenvolvimentismo a qualquer custo cria uma resposta irracional que ameaça atividades de alta renda econômica, como agricultura, turismo e pesca esportiva. com essa tese, esperamos informar outros pesquisadores, formuladores de políticas e a ampla audiência sobre a situação atual dos ecossistemas aquáticos e sobre possíveis alternativas.

Palavras-Chave: Homogenoceno, traços funcionais, Floresta Atlântica, barragem, invasores, Antropoceno

ABSTRACT

While you are reading this abstract, damming and introduction of non-native fish are threatening the global fish biodiversity by causing the loss of species and functional groups in aquatic environments. Even in highly diverse ecosystems, such as the neotropical floodplains, an increase in the number of introduced species does not imply higher biodiversity. Biological invasions, domination by bottom-feeding species (benthification), oligotrophication, and trophic downgrading are key processes threatening fish biodiversity. We compared the abundance of bottom- and- pelagic- feeders and top- predators in fresh waters of the world (lakes and reservoirs). We also combined 18 years (2000-2017) of fish captures (organized in functional groups) by nets and seines in the upper Paraná river floodplain to describe how biotic homogenization is shaping the biodiversity, even with the maintenance of the number of species. We are shown a replacement of natives by few and widespread functional groups and non-native groups. It generated redundancy in various metrics of biodiversity, such as biomass, size, density (BSD-approach), and food web interactions. The patterns found here reflected the domination by bottom-foraging (benthopelagic and demersal, the benthification process), intermediate (the “mesopredators release”), and non-native individuals. We should be aware that few groups replacing many rare functional groups and species disturb fresh waters in a very predictive way, by causing the loss of biodiversity from the populations to the ecosystem. An immediate consequence of the biotic homogenization in fresh waters is the collapse of the fisheries, the loss of environmental (water) quality, and the disappearance of crucial ecosystem services (e.g., control of pests, detritus cycling, and dispersion of plants). The developmentalism at any cost creates a non-rational feedback that threatens activities of high economic income, such as agriculture, tourism, and sport fisheries. Through this thesis, we hope to inform other researchers, policymakers, and the broad audience about the ongoing status of aquatic ecosystems and about possible alternatives.

Keywords: Homogenocene, traits, Atlantic Forest, reservoir, invaders, Anthropocene

SUMMARY

CHAPTER I

Redundancies and divergences of fish communities in a neotropical floodplain, a time-series under scrutiny

Abstract

Modern research evaluating trends of biodiversity must include the human influence as a key proxy. Here, we aimed to correlate fish biomass (Bio), Size, and density (Dens), i.e., the "BSD approach", with human related effects in aquatic environments. We expected to find evidences of two conspicuous effects in neotropical river floodplains: biotic homogenization and biological invasions, which can be characterized in different forms. We measured BSD of functional groups, according to habit (benthopelagic, demersal, and pelagic), origin (native, non-native), and trophic levels (TL2 to TL4) through time (2000-2017) in the Paraná river to test the effects of recent hypothesis linked to biotic homogenization and invaders (benthification, oligotrophication, and trophic downgrading). We represented our trends with simple parametric tests (regression, t- test) after transforming BSD values to the log-scale in order to focus in robust answers to our test of hypothesis. The BSD values variated for depending on the method of capture (nets or seines), but, generally, the Bio increased for common functional groups (i.e., benthopelagic in low and intermediate TL) and few common species. Demersal and non-native fish increased in Size, while pelagic and TL4 decreased in Size but increased in Dens. Since most results were as deterministic as we expected in our hypothesis, we accomplished our expectations, which means that benthification, oligotrophication, and trophic downgrading processes determined the abundance of fish species in the Paraná river floodplain. Such processes are linked to the enemy release, short-term adaptation of invaders, trophic interactions between native and non-native species, and environmental influence (flood pulse), all resulting in biotic homogenization. We conclude about the role of the human species in shaping the biodiversity in aquatic environments, also suggesting a long- term and non-specific monitoring, based on BSD.

Introduction

Debates involving scientists for evaluating the causes and consequences of changes in the number of species inspired science since decades (Darwin 1859, Lindeman 1942, Paine 1966, Barrett and Odum 2006, Primack et al. 2018). The debate intended to find a way to deal with the human influence, based in the ethic of the society, a matter of interest of researchers and policy makers (Primack et al. 2018). For instance, some limitations of local studies with respect to global patterns (Gonzalez et al. 2016) put into questioning the evidence that the regional diversity persist by the turnover of local species (Vellend et al. 2017). In the course of time, moreover, the concept of biodiversity has been developing in ecology, incorporating but not limiting to species richness concept (Mouchet et al. 2010, Cadotte et al. 2011). The lack of accurate information could weaken the findings, but scientists agree that biodiversity is a result of the human influence (Primack et al. 2018), independently of the scale (Worm and Paine 2016). Biotic homogenization, the loss of biodiversity at any ecological level (McKinney and Lockwood 1999), is now a synonymous of Anthropocene (Crutzen and Stoermer 2000, Olden et al. 2018).

Threats such as biological invasions and resulting biotic homogenization (Ricciardi et al. 2017) are increasing the extinction rates (Costello et al. 2013b). The fate of the aquatic biodiversity cannot be uncoupled from the future of the Homo sapiens (Richter et al. 1996), particularly in South America, where biological invasions and aquaculture are leading threats to the fish biodiversity (Vitule et al. 2017, Bezerra et al. 2019). Therefore, modern research requires quantitative synthesis in long-term, involving the most available kind of data, this is, biomass, body size (Jennings et al. 2008), and number of individuals (Gallardo et al. 2016). In this chapter, we are using anthropogenic proxies of biotic homogenization as proxies of fish communities against such variables in a robust time-series.

Human activities are the leading cause of the success of intermediate trophic levels (Prugh et al. 2009) in detriment of top- predators (Estes et al. 2011). Such processes, respectively called the mesopredators release and the trophic downgrading were recently related to biotic homogenization and the success of invaders (Bezerra et al. 2018, 2019). In Brazil, the artisanal fisheries can collapse in fresh waters because of the fisheries at the industrial scale and environmental

alterations with indisputable impacts over the fish community (Agostinho et al. 2004). Still, fish communities are frequently threatened by doubtful political choices and regulations controlling activities such as aquaculture and fisheries (Sampaio et al. 2015, Padial et al. 2017, Lima Junior et al. 2018).

The impoundment of rivers can assist the population with water and energy supplying, but it causes impacts to the local inhabitants (Petrere 1996) and to the native fish community (Skóra et al. 2015). Fisherman are now suffering from economic and health problems because they are obligated to change their methods and feeding habits (Cetra and Petrere Jr 2001, Petesse and Petrere 2012), or even to migrate to other activities (Carvalho 2008). Still, the Paraná river floodplain relies in the largest remnant of Atlantic Forest in South America and remains a target environment to the local economy, as well as to the community, researchers, and tourists (Agostinho et al. 2005), particularly after environmental alterations such as damming and introduction of non-native species.

As a result of impoundments, the retention of organic nutrients in reservoirs doubled from 1970 to 2000 (Maavara et al. 2015), also resulting in the introduction of non-native and invader species (Vitule et al. 2012, Pelicice et al. 2015). Both oligotrophication and introductions are associated to the limiting role of the pelagic food chain (Anderson et al. 2005, Bezerra et al. 2018). Even if pelagic predators are controlled from the bottom or from the top, they are probably most affected by the collapse of the nutrients after the dam, which restricts the primary and secondary production in the water column (Anderson et al. 2005). Oligotrophic states are related to cascading effects of invaders towards bottom-up dynamics resulting from human activities, which can also alter the pelagic food web towards an increase in the zooplankton/phytoplankton biomass ratio (Anderson et al. 2005). The benthification process (Mills et al. 2003, Mayer et al. 2014) results from the dominance of bottom-feeding fish, more than expected naturally (Bezerra et al. 2018). As we are shown in the chapter III, benthification and oligotrophication result from the dominance of bottom-feeding species in altered environments, particularly under influence of reservoirs, a source of non-native propagules (Gallardo et al. 2016) .

In the Paraná river, recent investigations of fish communities highlight common aspects of biodiversity, such as flood effects on reproduction (Agostinho

et al. 2004), recruitment (Oliveira et al. 2015), and associated ecological dynamics (Pereira et al. 2017), from populations to metacommunities (Padial et al. 2014). By monitoring the biomass, size, and density of fish individuals organized in functional groups, we investigated whether the abundance of fish varied in captures between 2000 and 2017, following the process of oligotrophication and benthification. We tested explicitly the abundance (biomass, density, and size) of fish species against the effects of biological invasions, biotic homogenization, and trophic downgrading.

Classic papers (e.g., Richter et al. 1996) introduced the way by which scientists should evaluate human impacts on aquatic ecosystems, which depends in great part on how the researcher define and organize biodiversity. We expected that human alterations such as damming (Agostinho et al. 2016) and introductions (Vitule et al. 2012) influenced the habit (i.e., habitat occupation, interactions, and reproduction) of fish species adapted to lotic conditions at the Paraná river floodplain in the long-term (Agostinho et al. 2004, Thomaz et al. 2007, Mormul et al. 2012, Padial et al. 2012, 2014), and that functional groups would answer gradually and differentially to the decrease of flood peaks (Ligon et al. 1995) and to the introduction of fish species (Júlio Júnior et al. 2009, Vitule et al. 2012, Daga et al. 2016), from 2000 to 2017. These processes would be reflected by a decrease and an accumulation around the average biomass and number of pelagic fish (a decrease in biodiversity), while bottom-feeding species (benthopelagic and demersal) increase in abundance, particularly, non-natives, due to evolutive advantages of introduced species (Keane and Crawley 2002). By following these deterministic changes, both benthification and oligotrophication processes could reflect short- term changes in the abundance of functional groups. We also expected that biomass and size of high TL decreased in consequence of the trophic downgrading (Estes et al. 2011), while the density of low TL increased by the influence of invaders.

Methods

We analyzed fish communities captured by nets and seines, from 2000 to 2017, in the Paraná river floodplain. Trimonthly, the staff of the Long-Term Ecological Program of the State University of Maringá (UEM, Brazil) sampled lagoons (27 lagoons) and rivers (Baía, Ivinhema, Paraná) of the Paraná river floodplain, each sampling with 1000 m² of gill nets (from 2.4 cm to 16 cm among knots) in a range of biotopes and, in average, 205 m2 of beach seines (0.5 cm among knots, 678 captures). Further details of the sampling program are available in the recent literature (Ceschin et al. 2018) and in the <peld.uem.br>. We classified the fish community in guilds of functional groups, in order to represent their biomass, size, and density by sample. Functional groups were divided by origin -- native and non- native (Langeani et al. 2007, Júlio Júnior et al. 2009, Ota et al. 2018), habit -- benthopelagic (benpel), demersal (dem), and pelagic (pel), and trophic levels -- TL2 to TL4 (Froese and Pauly 2016).

To evaluate biomass variation in the floodplain in each sampling, we calculated the biomass (g.m-2, variable “Bio”) as the sum of weights per sampled area in nets or seines, and the final value is the log transformed. The captures were standardized by effort (area of nets or seines), local, period, thus resembling a Capture per Unit of Effort (CPUE). Therefore, the long-term evaluation of CPUE was a proxy of biomass. The “Size” was the average weight in capture by fish species, also in a log-scale, and the density “Dens” was the log- scale number of individuals per sampled area, a proxy of number of individuals.

We evaluated linear trends (regression, student’s t-test, from 2000 to 2017) of several statistic parameters of the log- normal distribution of Bio, Size, and Dens (now referred by the acronym BSD): average, inter-quartile range (IQR), maximum, median, standard deviation (sd), and variance (var). Measures of central tendency, average and median, represented the average trend of BSD through time, while dispersion measures IQR, sd, and var represented the diversity of BSD. We removed redundant parameters, always maintaining the stronger tendency (higher t-value). We have chosen the strongest trend when average and median represented the same trend (positive or negative), or when var (or other dispersion measure) followed the trend represented by sd (frequently the higher t-value), otherwise both were reported.

Because benthopelagic groups in TL2 dominated the captures, we also evaluated rare species. Rarity varies depending on the research approach (Gaston and Kunin 1997, Gotelli and Colwell 2001, Padial et al. 2012, Siqueira et al. 2012). We defined common and rare species based in the Bio and Dens (Brown 1984) of the individuals. Commons were those within the IQR of Bio and higher than the fourth quartile of the Dens distribution. Rare species were lower than the first or higher than the fourth quartiles of the Bio distribution, and always lower than the first quartile of Dens. While defining rarity only through the time, we avoided obvious sampling effect expected from the definition or rarity in the space (Brown 1984), this is, the patchy distribution of commons and higher sampling error expected for rare. It was also the reason for representing functional groups yearly, instead of seasonally.

Results

The monitoring of nets (2000-2017) resulted in the capture of 155,145 individuals (average individual weight 160 g, 135 fish species) and 187,641 individuals (average individual weight 2.51 g, 110 fish species) in seines, totalizing 159 species. Despite co- occurrences, communities captured in nets were different of seines (Figure 1). In nets, general BSD trends were positive, and most of the community was composed of benpel individuals (Table1, Table SM1). As most groups increased in BSD through the time, median Bio (coefficient (b) = 0.037 ± 0.007; $P < 0.001$), Size (b = 0.018 ± 0.01; P = 0.06), and Dens (b = 0.020 ± 0.006; P = 0.001), as well as Bio-and-Dens-dispersion (see dispersion of Bio and Dens), increased at the community level.

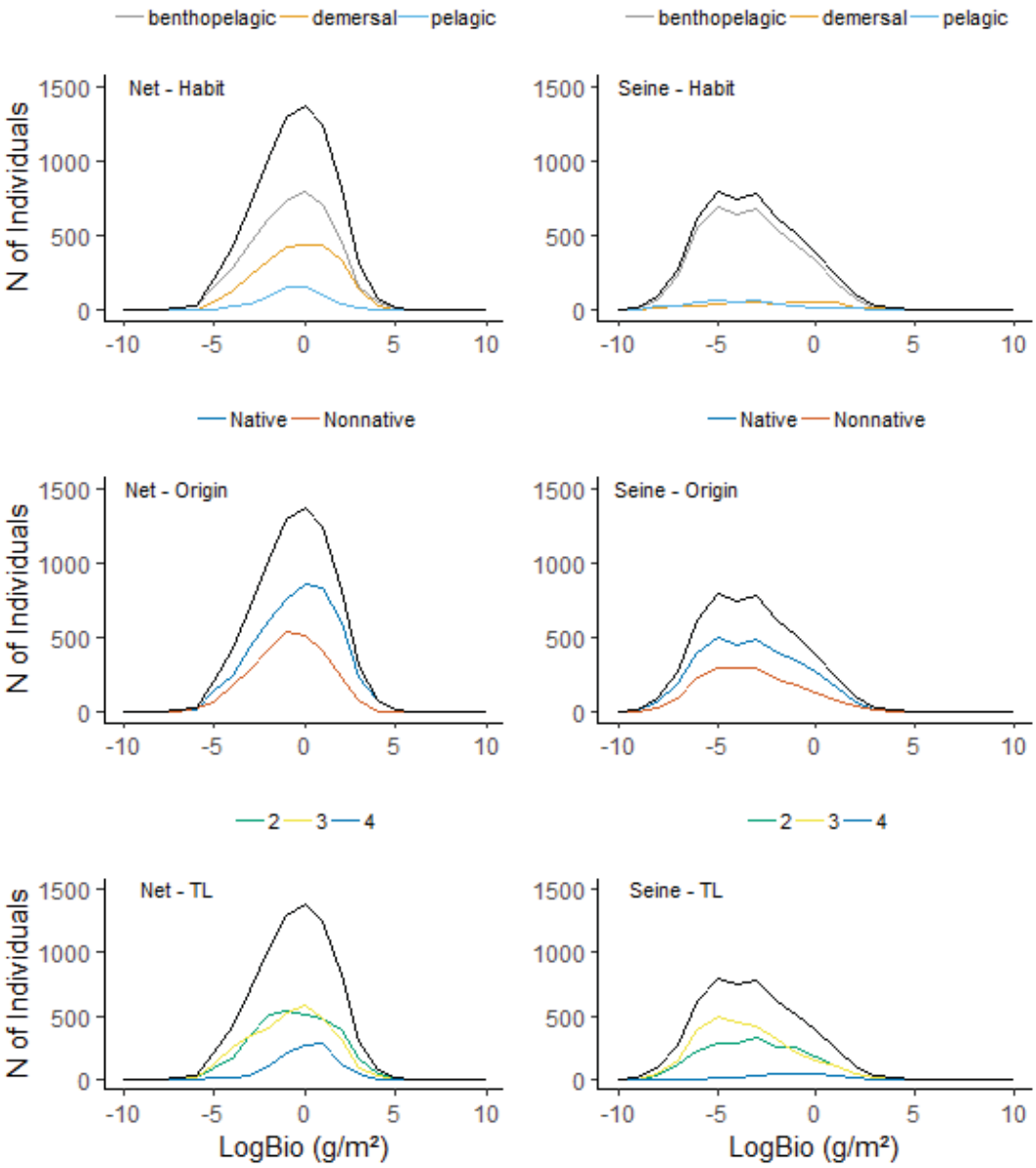


Figure 1. Distribution of fish biomass in a log scale (LogBio) in the Paraná river floodplain, based in the number (N) of individuals. Net and seine captures are categorized according to habit, origin, and trophic level.

Table 1. Biomass (Bio), Size, and Density (BSD, represented by – maximum (max), average and median values) and BSD-variation (dispersion parameters – Inter-Quartile Range (IQR), standard deviation (sd), and variance (var)) for individuals captured in nets and seines in the Paraná river floodplain from 2000 to 2017. Other statistics are the estimated coefficient (b) and the Standard Error (SE). We classified groups by origin (native, non-native), habit (Benpel- benthopelagic, Dem- demersal, and Pel- pelagic), and trophic level (TL). Only trends with $P < 0.05$ of nets or seins are shown. For the complete table, please access the Supplementary Material (Table SM1).

Groups		Net				Seine			
		b	SE	*t*-value	*P*-value	b	SE	*t*-value	*P*-value
Biomass									
Community	max	**0.039**	**0.017**	**2.294**	**0.025**	-0.049	0.036	-1.353	0.181
	median	**0.037**	**0.007**	**5.69**	**0.001**	-0.023	0.016	-1.392	0.169
	var	**0.038**	**0.015**	**2.468**	**0.016**	-0.04	0.034	-1.18	0.242
Native	max	**0.038**	**0.018**	**2.104**	**0.039**	-0.069	0.041	-1.667	0.1
	median	**0.041**	**0.009**	**4.721**	**0.001**	-0.008	0.02	-0.416	0.679
Nonnative	max	**0.024**	**0.011**	**2.135**	**0.037**	-0.034	0.039	-0.867	0.389
	median	**0.034**	**0.009**	**3.801**	**0.001**	-0.052	0.021	-2.405	0.019
	IQR	0.021	0.011	1.957	0.055	-0.042	0.021	-2.03	0.047
	sd	**0.011**	**0.004**	**2.825**	**0.006**	-0.017	0.01	-1.63	0.108
Benpel	max	**0.07**	**0.02**	**3.611**	**0.001**	-0.07	0.038	-1.829	0.072
	median	**0.051**	**0.009**	**5.566**	**0.001**	-0.019	0.016	-1.192	0.238
	sd	**0.018**	**0.005**	**3.977**	**0.001**	-0.008	0.009	-0.952	0.345
Dem	IQR	-0.02	0.014	-1.422	0.16	**-0.102**	**0.04**	**-2.54**	**0.014**
Pel	IQR	**-0.045**	**0.017**	**-2.586**	**0.012**	**0.089**	**0.033**	**2.66**	**0.01**
TL2	median	**0.081**	**0.007**	**11.238**	**<0.001**	-0.044	0.023	-1.962	0.054
TL3	sd	**0.011**	**0.005**	**2.317**	**0.024**	-0.008	0.009	-0.876	0.384
Size									
Community	average	**0.016**	**0.004**	**4.032**	**<0.001**	0.001	0.014	0.011	0.991
Native	median	**0.024**	**0.006**	**4.265**	**<0.001**	0.013	0.016	0.793	0.431
	var	-0.008	0.007	-1.102	0.275	**0.119**	**0.046**	**2.597**	**0.012**
Nonnative	median	**0.024**	**0.006**	**3.636**	**0.001**	-0.021	0.014	-1.509	0.136
Benpel	median	**0.022**	**0.005**	**4.069**	**<0.001**	0.007	0.011	0.603	0.549
Dem	median	**0.016**	**0.006**	**2.518**	**0.014**	0.053	0.048	1.115	0.269
Pel	max	**0.039**	**0.013**	**3.139**	**0.003**	-0.027	0.066	-0.414	0.68
	median	0.011	0.009	1.158	0.251	**-0.179**	**0.044**	**-4.081**	**<0.001**
	sd	**0.015**	**0.007**	**2.199**	**0.032**	-0.041	0.028	-1.493	0.142
TL2	average	**0.033**	**0.005**	**6.829**	**<0.001**	0.028	0.02	1.421	0.16
	var	**-0.031**	**0.008**	**-4.166**	**<0.001**	**0.284**	**0.056**	**5.042**	**<0.001**
TL3	max	**0.063**	**0.015**	**4.334**	**<0.001**	-0.018	0.047	-0.380	0.705
	IQR	0.012	0.01	1.209	0.231	**-0.063**	**0.023**	**-2.790**	**0.007**
	sd	**0.009**	**0.003**	**2.835**	**0.006**	-0.013	0.012	-1.008	0.317
TL4	median	0.001	0.008	0.133	0.894	**-0.124**	**0.041**	**-3.029**	**0.004**
	var	**0.032**	**0.013**	**2.41**	**0.019**	-0.052	0.086	-0.605	0.548
Density									
Community	median	**0.020**	**0.006**	**3.355**	**0.001**	-0.011	0.011	-1.049	0.298
	IQR	**0.025**	**0.007**	**3.442**	**0.001**	-0.028	0.014	-1.974	0.053

Native	max	0.009	0.021	0.455	0.651	**-0.102**	**0.041**	**-2.519**	**0.014**
	average	**0.022**	**0.006**	**3.468**	**0.001**	-0.015	0.011	-1.344	0.184
	IQR	**0.022**	**0.007**	**3.412**	**0.001**	-0.031	0.017	-1.771	0.081
Benpel	average	**0.020**	**0.006**	**3.307**	**0.002**	-0.015	0.01	-1.440	0.155
	IQR	**0.031**	**0.007**	**4.085**	**<0.001**	**-0.033**	**0.015**	**-2.196**	**0.032**
Dem	median	**0.015**	**0.007**	**2.130**	**0.037**	-0.016	0.021	-0.761	0.449
Pel	max	-0.002	0.022	-0.109	0.913	**0.194**	**0.04**	**4.817**	**0.001**
	median	0.001	0.012	-0.022	0.983	**0.076**	**0.023**	**3.317**	**0.002**
	IQR	-0.004	0.011	-0.325	0.747	**0.077**	**0.021**	**3.688**	**<0.001**
TL2	max	-0.01	0.017	-0.573	0.568	**-0.167**	**0.039**	**-4.289**	**<0.001**
	average	**0.029**	**0.004**	**6.769**	**0.001**	**-0.041**	**0.012**	**-3.499**	**0.001**
	sd	**0.008**	**0.003**	**2.549**	**0.013**	**-0.020**	**0.009**	**-2.245**	**0.028**
TL4	max	**0.05**	**0.025**	**2.019**	**0.048**	0.085	0.054	1.564	0.124
	average	**0.016**	**0.008**	**2.049**	**0.045**	0.045	0.022	2.001	0.051
	var	**0.026**	**0.01**	**2.525**	**0.014**	-0.032	0.095	-0.331	0.742

On other hand, the capture in seines had mainly negative BSD- trends. In seines, the maximum Dens of natives (b = -0.102 ± 0.041; P = 0.014) and TL2 (b = -0.167 ± 0.039; P = 0.014) decreased. Alternatively, average and max values of Dens of pelagic individuals (average b = 0.081 ± 0.021; P < 0.001; max b = 0.194 ± 0.040; P < 0.001) and their Bio- and Dens- dispersion increased in recent years. Independently on the method, the Dens of pelagic and the Bio of non-natives increased, with decreasing Size of pelagic and TL4 individuals (seines). Once temporal patterns of BSD hanged on the method of capture, we treated net and seine separately, according to habit (Figure 2), origin (Figure 3), and TL (Figure 4). Benthopelagic, natives, and demersal had broader dispersion of Bio and Dens values, while non-native, pelagic and TL4 had a higher Bio and Dens, on average, considering nets, seines, and most of the years.

In general, biomass agreed with Dens trends, except for the Bio of non-natives in nets, that increased with Size through the time (Figure 5). Non-native species accounted for 40% of the number of species, and increased in recent years, despite the number of species did not vary (Figure 6).

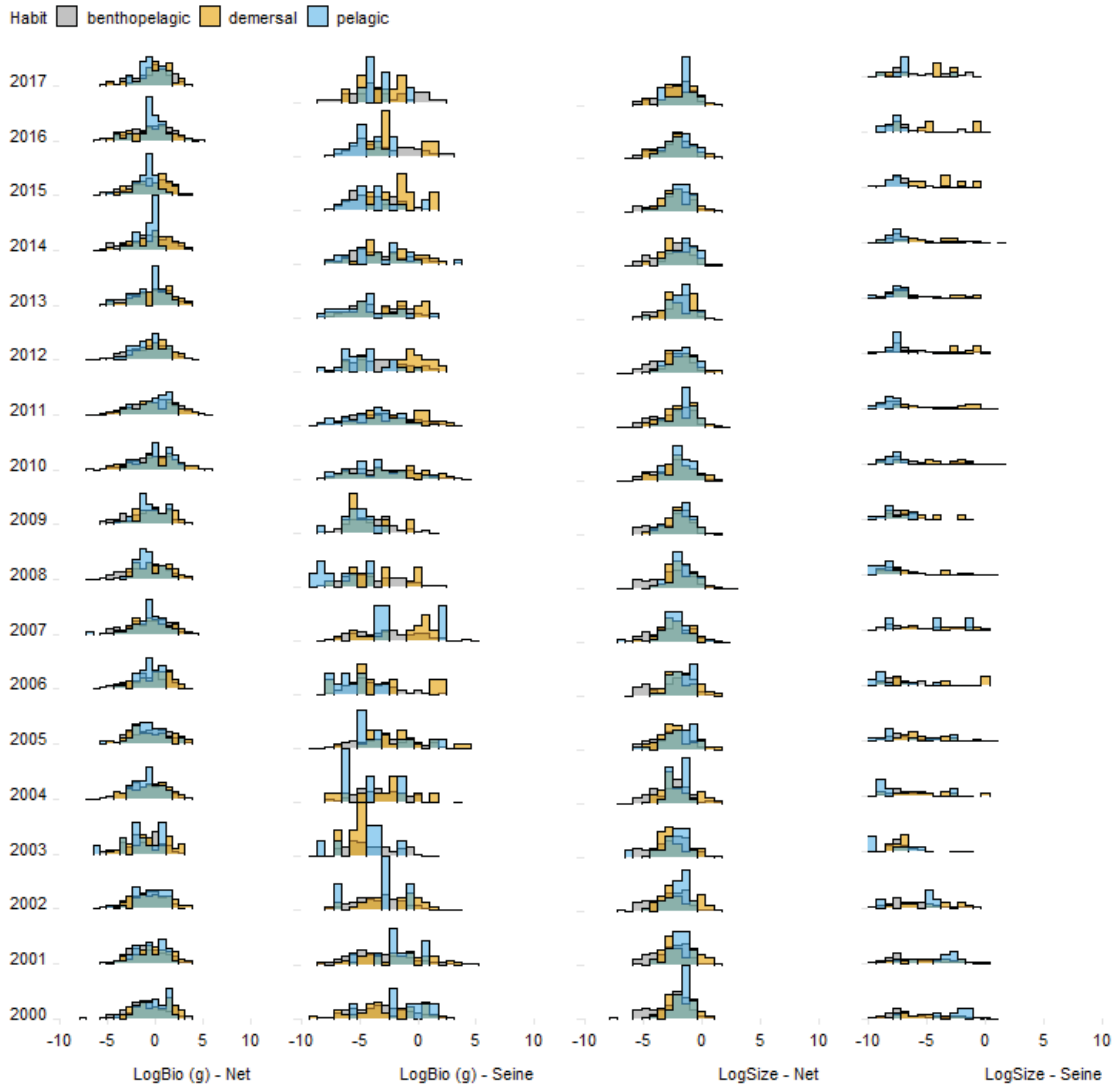


Figure 2. Yearly (2000-2017) distribution of log-scale biomass (LogBio) and log-scale size (LogSize) of fish captured by nets and seines in the Paraná river floodplain. Colours represent habits.

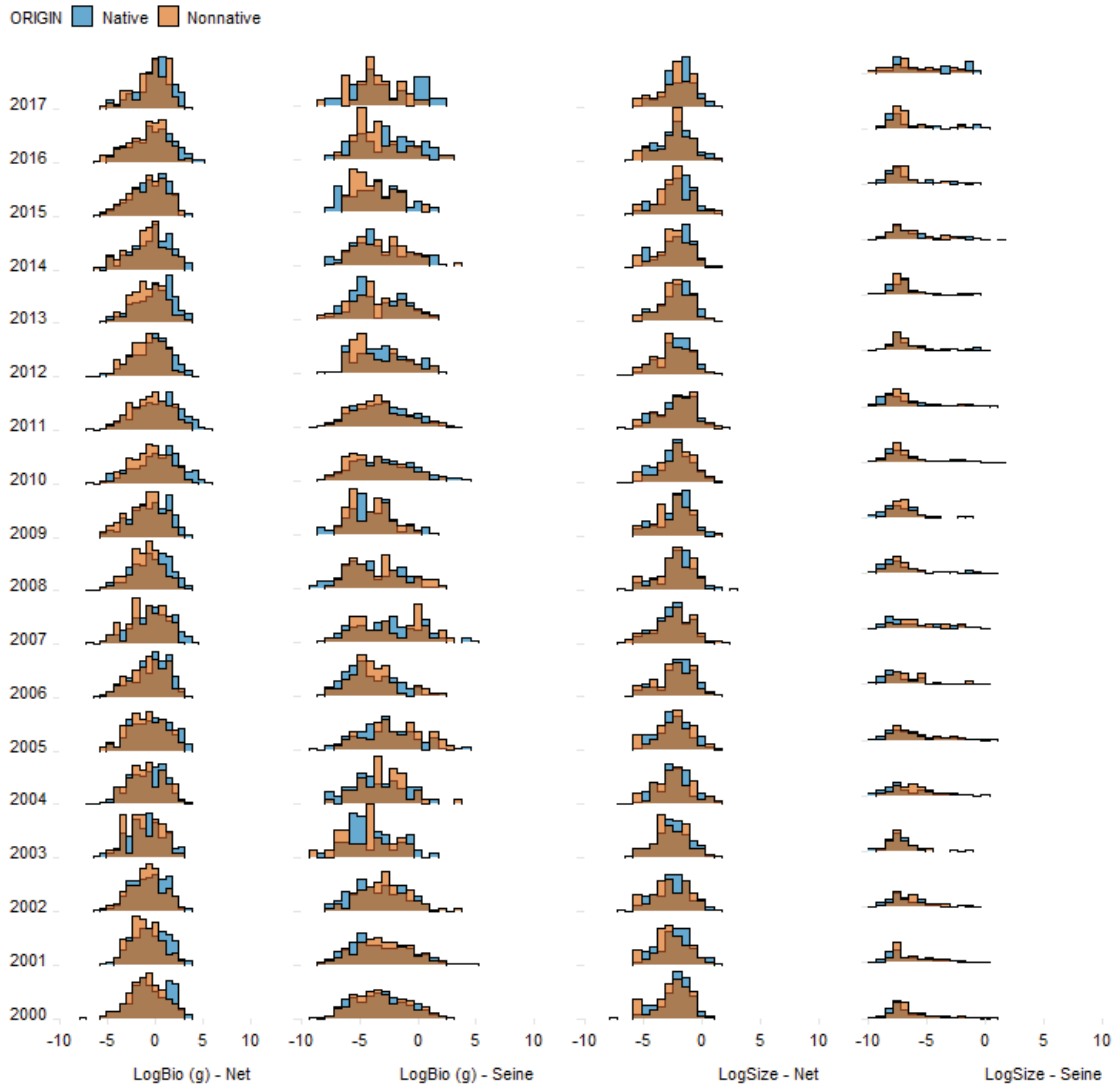


Figure 3. Yearly (2000-2017) distribution of log-scale biomass (LogBio) and log-scale size (LogSize) of fish captured by nets and seines in the Paraná river floodplain. Colours represent origin.

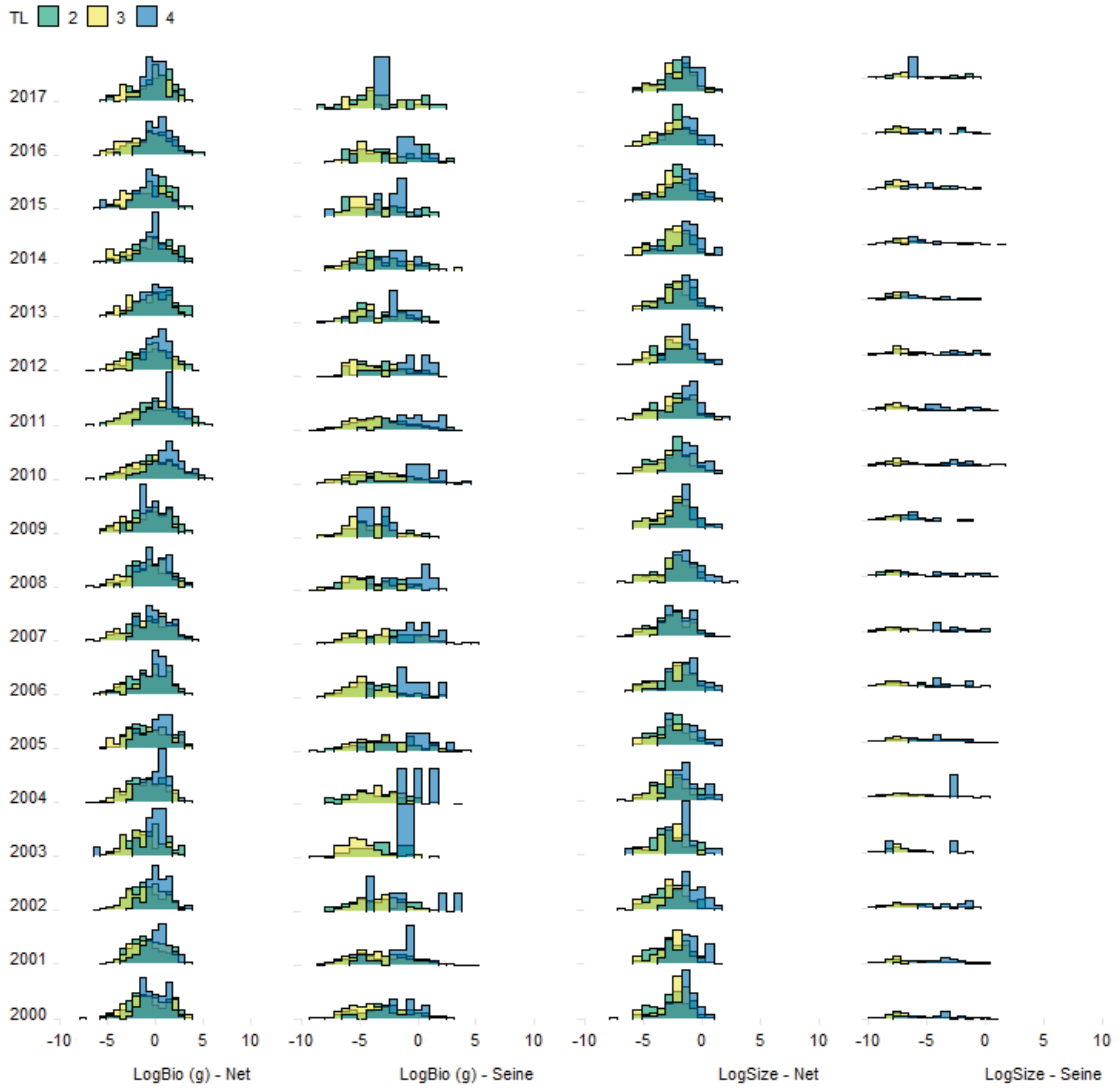


Figure 4. Yearly (2000-2017) distribution of log-scale biomass (LogBio) and log-scale size (LogSize) of fish captured by nets and seines in the Paraná river floodplain. Colours represent trophic levels.

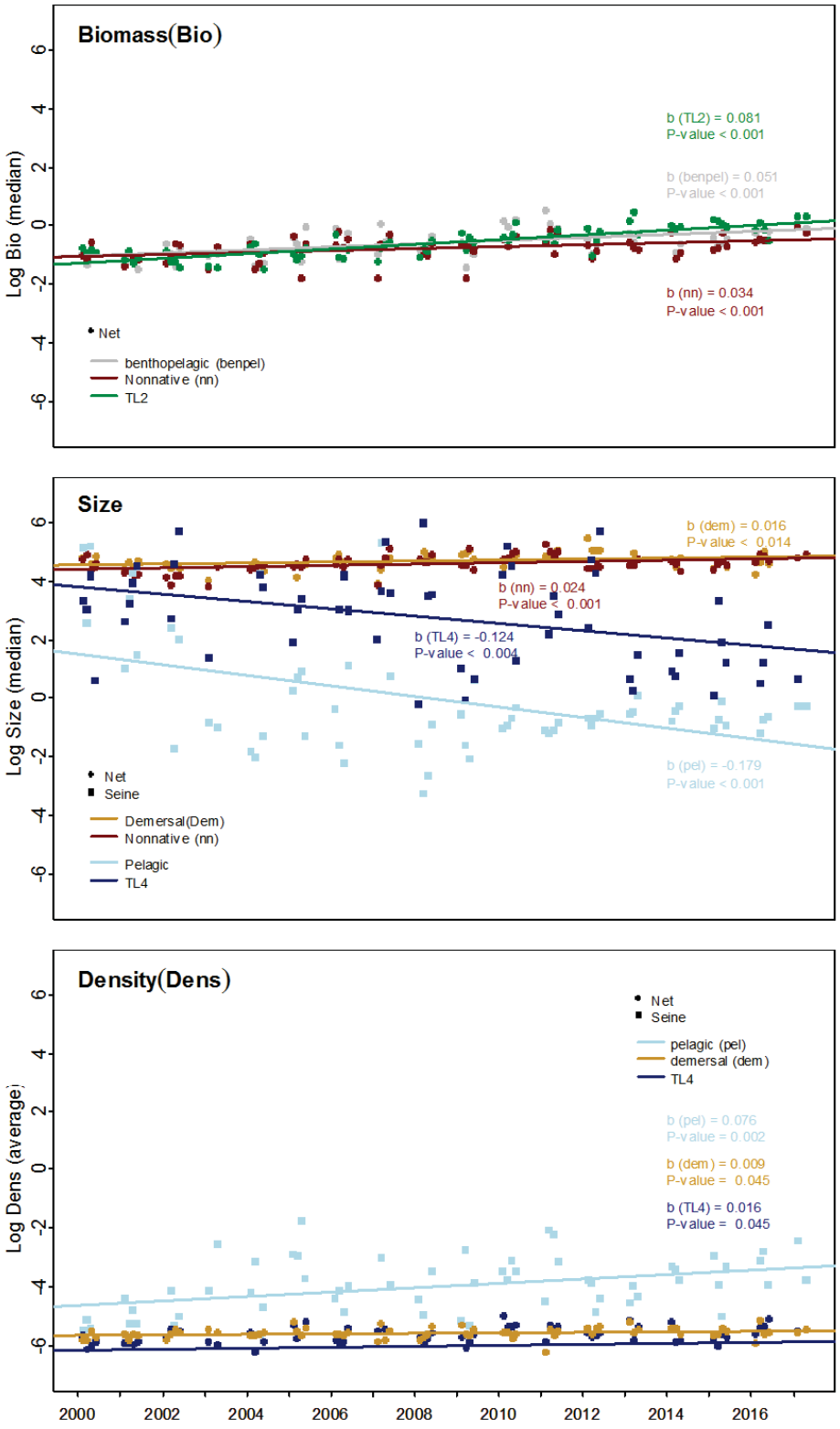


Figure 5. Trends of Biomass (Bio), Size, and Density (Dens) of fish communities captured in nets (cross) and seines (square), from 2000 to 2017, in the Paraná river floodplain (net captures).

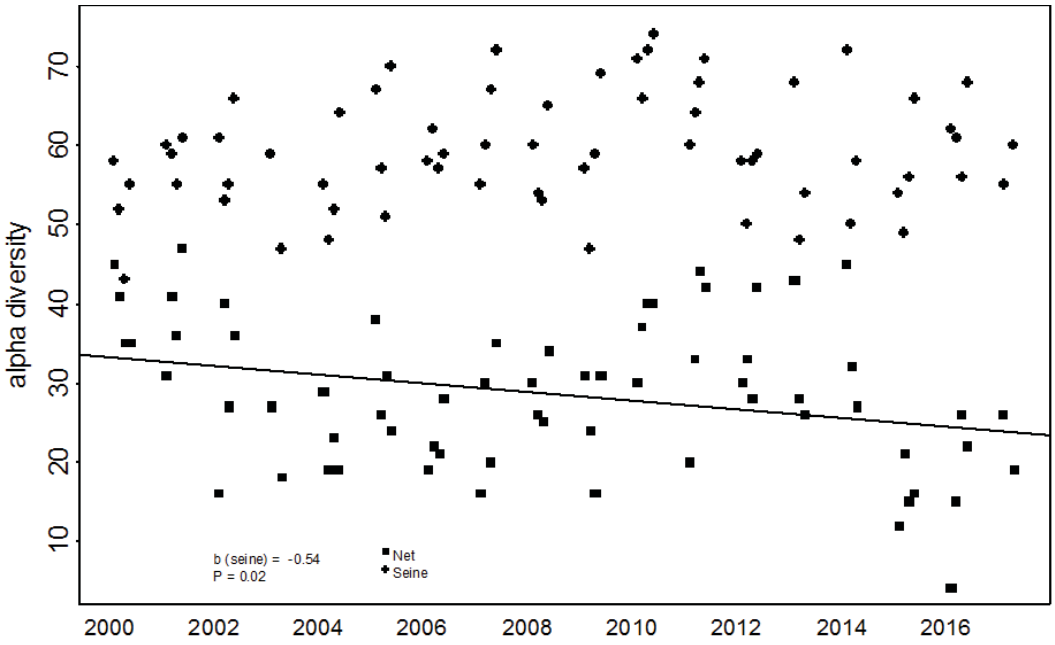


Figure 6. Number of fish species captured in nets (cross) and seines (square), yearly, from 2000 to 2017, in the Paraná river floodplain.

Few common (Figure 7) and rare (Figure 8) species increased in biomass, while many rare species decreased in biomass. Trends of few non-native species in TL4 such as *Astronotus crassipinnis* (Heckel, 1840) and Cichla spp., co-occurring with non-native "Piranhas" of the genus Metinnys, both positively correlated with Bio and Size of non-native communities. Again, common and rare non-natives were frequent in the most recent years. Few common in TL2 included also native species, the streaked prochilod *Prochilodus lineatus* (Valenciennes, 1837) and *Serrapinnus heterodon* (Eigenmann, 1915).

Figure 7. Common and rare benthopelagic fish species (colours) in the trophic level 2, according to their occurrence in the Paraná river floodplain (2000-2017). Common occurrences rely within the IQR of the biomass (Bio) distribution and in the upper 25% distribution of the density (Dens) distribution. Species names are abbreviated (full name available at the Supplementary material, Table SM2). Lines represent tendencies with $P < 0.05$.

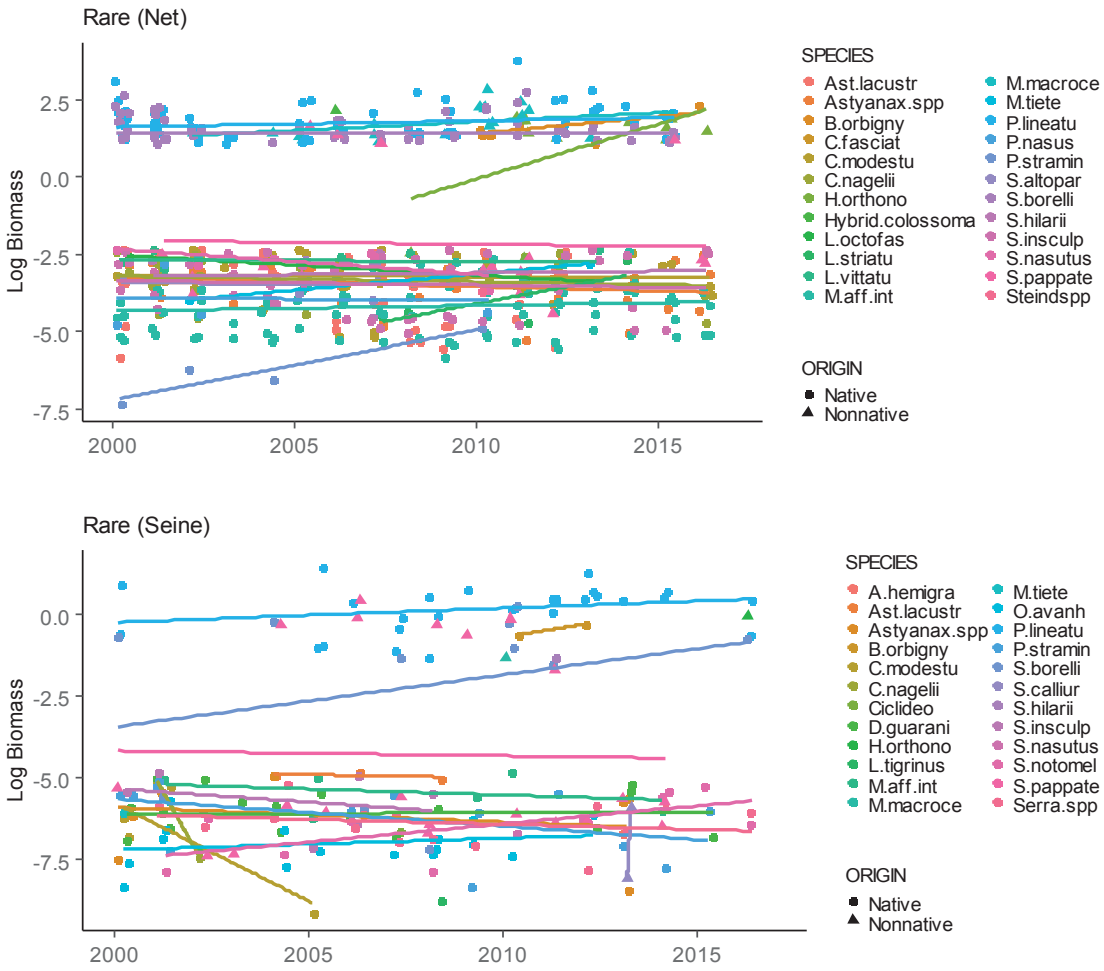


Figure 8. Rare benthopelagic fish species (colours) in the trophic level 2, according to their occurrence in the Paraná river floodplain (2000-2017). Rare occurrences rely in the first or in the last quartile of the biomass (Bio) distribution, and in lowest 25% of the density (Dens) distribution. Species names are abbreviated (full name available at the Supplementary material, Table SM2). Lines represent tendencies with $P < 0.05$.

Discussion

Here, we elucidated aspects of the community assembling by using different sampling methods and simple analytic procedures, confronting expected effects of human- related threats (highlighting the presence of non-native species) to the fish biodiversity with the abundance of native and non-native fish species. We detailed how the domination by few and common functional groups (benthopelagic in TL2) and species (e.g., *P*. l*ineatus*) triggered an increasing biomass and density at the community level, while the abundance of many rare and native species decreased. In summary, we did find few winners and many losers in long term trends of fish communities in a major Neotropical floodplain (McKinney and Lockwood 1999, Vitule et al. 2012, Toussaint et al. 2016a, Olden et al. 2018). As we expected, biomasses increased as a result of the presence of larger benthopelagic, non-native, and demersal individuals in recent captures, independently on the sampling method (net and seine). The density of pelagic and the size of non- natives and TL4 followed the pattern expected in the benthification (see chapter III) and trophic downgrading (Estes et al. 2011) hypotheses. The domination by few common species and functional groups (i.e., benthopelagic in TL2 and TL3) represented biotic homogenization (McKinney and Lockwood 1999) reliant on the habit and on the origin of fish species.

However, as benthopelagic and demersal individuals answered deterministically to our surrogates, expected trends for non-native and pelagic species were not completely accomplished, and varied depending on the sampling method. Therefore, dynamics cannot be explained merely by the benthification, oligotrophication, and trophic downgrading. Other short-term adaptation on the life history of fish species may also drive the assembling of fish community (Lundberg et al. 1998, Thompson 1998, Parmesan 2006, Olden et al. 2018). Even so, such adaptations are directly (Winemiller et al. 2014, Skóra et al. 2015) or indirectly (Hoeinghaus et al. 2009) related to the controlling of the flood pulse (Junk et al. 1989) by the Itaipu and Porto Primavera reservoirs, built in 1982 and 1997, respectively (Petrere 1996, Langeani et al. 2007, Júlio Júnior et al. 2009, Vitule et al. 2012, Bailly et al. 2016). Also, many other smaller reservoirs regulate the peak of floods in the Paraná river and in other floodplains (Ligon et al. 1995), which decreases the reproductive success of migratory native species, such as previously observed in the Paraná river (Gubiani et al. 2007, Fernandes

et al. 2009, Oliveira et al. 2015). Still, periods of rainfall are followed by short floods (Thomaz et al. 2007). In strong flood periods (such as in 2007, 2010 and 2011), many water bodies (rivers, lagoons, and channels) are connected, and the beta-diversity in the floodplain decreases due to mass effects (Thomaz et al. 2007, Padial et al. 2014, Ceschin et al. 2018). Accordingly, we observed an increased Bio and Dens, as well as Bio- and Dens- dispersion in years of flood, but the number of species did not vary in nets. It means that abundance can be a better indicator of biodiversity of native and non-native species than the number of species.

The loss of biodiversity was recently evidenced by a decreasing beta-diversity associated with the control of the flood pulse, oligotrophication, and influence of aquatic macrophytes in the Paraná river floodplain (Ceschin et al. 2018). Here, we contributed with new evidences, now related to abundance, and focused on the success of non-natives in low TL, in the most recent years of study. Since the fish community of the Paraná river was historically composed by large predators, now replaced by intermediate trophic levels, we portrayed a classic scenario of trophic downgrading (D'Alelio et al. 2016, Olden et al. 2018). Also, the homogenization process (McKinney and Lockwood 2001) was a consequence of the good fitness of low-and-intermediate-predators in the adult phase (demersal and non-natives, particularly), and low reproductive success of rare species, configuring a "meso-predator release" (Prugh et al. 2009). Therefore, such process could also be linked to biotic homogenization (Vitule et al. 2012) and biological invasions (Lövei and Lewinsohn 2012), which can cause mass effects, the enemy release (Keane and Crawley 2002), and influence trophic interactions (Sih et al. 2010, Pintor and Byers 2015).

The release of non-natives, or the enemy-release (Keane and Crawley 2002) was evident due to the replacement of native by non-native species, maintaining the diversity and increasing the abundance of the community in low TL. Still, non-native prey can contribute to the success of native predators (Pintor and Byers 2015). In both hypothesis, non-natives could be the reason for the success of the native fish community in the floodplain (Gozlan 2008). If non-natives were supporting fish in TL2 while they are the reason for the success of the fish community, the trophic downgrading explains the success of the fish community in terms of abundance. Nevertheless, we argue that the replacement

of natives by non-natives is probably the worst aspect of the biotic homogenization in the Paraná river floodplain (Vitule et al. 2012). The domination by few common species and the success of non-natives raises a great concern about intentional and unintentional introductions related to aquaculture, fisheries, fish stocking programs, and its related impacts (Ortega et al. 2015, Padial et al. 2017).

In general, non-natives prospered in the past decades (Skóra et al. 2015), representing 40% of the captured species. The temporal trends of non-natives highlighted here agree with the intensification of intentional introductions due to aquaculture (Nobile et al. 2018) and fish stocking policies in rivers (Agostinho et al. 2008) and in reservoirs (Agostinho et al. 2016) in Brazil. Fish farming targets non-native fish species with rapid growth, but they did not find a way to avoid escapes (Vitule et al. 2009). Non-native meso-predators have the potential to change the diet of native preys (Mormul et al. 2012). Such species are now interbreeding with the native biota and hybrids are increasing (Prado et al. 2012). The new introductions may change overall features of fish communities, periods of flood can be more critical because they increase the likelihood of escapes from surrounding local fish farms (Ortega et al. 2015), particularly few non- native associated to biotic homogenization.

Few functional groups and species hindered the decreasing biomass of many rare species and functional groups. Some pelagic species inhabited the nearshore zone in association with plants and macrophytes (Agostinho et al. 2007, Schultz and Dibble 2012), therefore their dependence on the pelagic food chain is not restricted. Some of these macrophytes, e.g., *Hydrilla verticillata* (L.f.) Royle, are non-native and serve as a new foraging ground to small pelagic fish (Carniatto et al. 2014). It opens a window for specific approaches testing the effects of benthification and oligotrophication to complement our study. A size-based approach related to trophic interactions (Barnes et al. 2010, Giacomini et al. 2013) or an experimental approach with mesocosms should be encouraged.
Rare species may have an important structuring role to the ecosystem due to their usually unique functionality (Leitão et al. 2016). Managers sustain that relying the conservation on rare species is a dangerous strategy because many will disappear. In effect, it should be the opposite. The loss of rare species is an announced tragedy to the global ecosystems (Costello et al. 2013a). Such

species are more vulnerable because they have less reproductive fitness (Gaston and Kunin 1997). Therefore, their survivorship is crucial, ongoing with the development of human populations, which could be a good starting point to their conservation.

While describing a tendency for increasing size and density of the fish community, ongoing with the success of few species (highlighting non-natives), we added solid basis to the argument of biotic homogenization in freshwaters. We were successful in this task because we hanged on a floodplain system previously characterized by the influence of biotic homogenization due to the human influence (Agostinho et al. 2005, Thomaz et al. 2007, Júlio Júnior et al. 2009, Vitule et al. 2012, Ceschin et al. 2018). This is, our intent was not to answer if there was biotic homogenization in the Paraná river floodplain, because such process is broadly reported in neotropical rivers (Petesse and Petrere 2012, Toussaint et al. 2016b, Vitorino Júnior et al. 2016, Bezerra et al. 2019), but how it affected the fish biodiversity in the past decades. Contrarily our expectations, nets and seines sampled different communities resembling a comparison between “offshore” vs. “nearshore” communities, commonly used in lakes (Kitchell et al. 2000, Gondwe et al. 2011, Paterson et al. 2014) and marine environments. Nevertheless, we do realize that it is not a direct assumption in rivers such as those in the upper Paraná river floodplain. In fact, seines were operated in nearshore biotopes where there are some species coexisting with macrophytes (Agostinho et al. 2007, Carniatto et al. 2014, Ceschin et al. 2018), many of which can disperse and can occupy the river channel (Schultz and Dibble 2012, Padial et al. 2014).

Also, we did not intend to represent all dynamics of all fish species in the ecosystem. One could argue that all devices used to fisheries are selective in some degree and some fish species have mechanisms to avoid the capture by nets and seines (Misund et al. 2008). However, a possible sampling effect for seines (Figure SM1) was smoothed for Bio and Dens as they were standardized by effort and for size by averaging the individual weight in the seasons. Still, we did suffer from the recurrent problem of sampling effort. Most of the groups which high abundance (native and benthopelagic in TL2 and TL3), or the common species, were those driving the dynamics. We smoothed this problem by evaluating each species separately.

We highlight the simplicity of our approach and encourage its replication in other ecosystems, particularly floodplains. We reinforce our sampling methods, that were standardized, always capturing fish in the same place with the same gears. We represented our trends as simple as possible, in order to avoid a complex statistical approach, but a robust test of hypothesis. It was a consequence of the appeal of respectful ecologists (Gonzalez et al. 2016, Vellend et al. 2017, Primack et al. 2018) to bring confidence to the field of Ecology with strong data-basis and robust and simple analysis. All procedures, from sampling of fish species to the writing of this manuscript, followed ethical guidelines expected for contributions to the science (Primack et al. 2018).

In conclusion, trends followed what we could expect from the effects of the human influence over the fish community, with expected effects of damming and introduction of non-natives controlling the functional diversity in the Paraná river floodplain. Even if our time window (18 years) was not enough to observe all expected effects of biotic homogenization, we generated evidences of the effect of the environmental alteration, dating from the 70's and 80's. Right after the most significant damming events, fish species probably adapted rapidly and maintained a less intense, but still significative, phenotypic answer (the one described here). We discussed a candidate mechanism of biotic homogenization (e.g., observed in artificial environments), the increase of size and density of benthopelagic and demersal species, while pelagic increase in density but decrease in size which could be the process explaining the higher abundance in low- and intermediate- trophic levels. Few native and non-native common species triggered the dynamics of the fish community, highlighting the success of big individuals of non-native species in recent years. The success of few widespread non-natives occurred at expenses of the fish biodiversity of the Paraná river floodplain, in the past two decades. Even so, native communities prospered by the increasing abundance of few species. Surprisingly, the Paraná river floodplain still preserves native species, which can be a good indicator of the efficiency of surrounding preserved areas.

CHAPTER II

Ecosystem effects of the water-regulation in a neotropical floodplain

Abstract

In the XXI century, the human species has established itself as the greatest force behind the environmental change. Damming and introduction of non-native species are amongst the most significant threats to the freshwater biodiversity. We investigated the role of the water level artificial control as a shaping force of trophic interactions in a floodplain river, and whether benthification and oligotrophication hypothesis explained the time-dynamic variation of the fish biomass in a neotropical floodplain. We grouped the functional biodiversity of fish species according to their habit (benthopelagic, demersal, and pelagic) and origin (native or non-native) in a size- based food web model of the Paraná river floodplain. We observed the influence of the water level as the main bottom-up forcing of the fish biomass, mainly by the dominance of intermediate and low trophic levels of native and non-native fish species which support high trophic levels in alternative states of the ecosystem. Pelagic species and visual predators benefits from the dry period, which is also linked to predators' size. The biomass of such piscivores and non-natives was less correlated to the water level variation, therefore the top-down control of pelagic piscivores, as well as the influence of top- predators on little individuals is more likely. This kind of mixed control was associated to the increase in the biomass of benthopelagic, demersal, and non-native fish species, however biotic homogenization explained only partially the observed patterns. The dominance by some pelagic predators was an externality of our approach related to the influence of Piranhas and small pelagic individuals. We conclude about the role of the water level as an environmental filter.

Introduction

The way by which ecologists propose the organization of biodiversity frequently define the outputs of their work. Ecologists using the concept of biodiversity beyond the number of species (Gotelli and Colwell 2001) superposed an historical barrier (Cernansky 2017) that blocked a representation of a range of properties inherent to the composition of biological entities (Soberón 2007,

Jennings et al. 2008). For example, niche and habitat were treated as synonymous in many studies until recently (Soberón 2007). As alternative facets of biodiversity arise, we are urged to join individual behaviour, biotic interactions, and environmental filters with the aim to inform the management (Coll and Libralato 2012) of patterns related to ecology and evolution (Pastor 2017, Rangel et al. 2018).

To date, one of the most feasible way to distinguish the compartmentalization of biodiversity is to analyze size and abundance. From individuals to ecosystems, and depending of the tested hypothesis, abundance answers questions in genetic (Miraldo et al. 2016), ecologic (Guénard and Legendre 2018), functional (Mouchet et al. 2010) multiple levels (Cucherousset and Villéger 2015). Monitoring the abundance of functional groups according to their size and life history, considering their interactions with another groups, is an efficient manner to understand the ecology and the evolution of individuals. In fact, trophic pyramids and size-based models are inter-changeable ways to represent life at the ecosystem level (Trebilco et al. 2013). It was tried before using size-based models (Jennings et al. 2008), trophic interactions based on size (Giacomini et al. 2013), functional ecology (Skóra et al. 2015), and niche-based models (Winemiller and Jepsen 1998). However, none of these approaches linked environmental filters, functional ecology (life-history), size-based models, and predation (explicitly in a logical matrix of interactions) together in an ecosystem approach. Here, we propose a summary on how these characteristics of functional groups have been linked to river changes.

In Neotropical environments, previous studies highlighted the trophic downgrading experimentally (Pendleton et al. 2014, 2015). They found that the predominance of bottom-up effects and the loss of rare species influenced ecosystem processes. However, such approaches did not consider important aspects of trophic interactions. What if the size of individuals triggered top-down effects to other functional groups?

The analysis of alternative states depends a lot on the scale and on the environmental complexity. If one aims to investigate the biodiversity at the level of riverine basin (Rodrigues-Filho et al. 2018), the River Continuum Concept (Vannote et al. 1980) is important. If the focus is a riverine stretch subjected to periodic floods, mostly in the same altitude, certainly, the Flood Pulse (FP)

concept is important (Junk et al. 1989). Indeed, there is no an ecosystem in the world free from the human influence (Crutzen 2006). In continental waters, the effect of damming and the presence of invaders must be accounted (e.g., Júlio Júnior et al. 2009, Vitule et al. 2012, Britton and Orsi 2012, Pelicice et al. 2015). In artificial environments, the human behaviour control food webs towards bottom-up dynamics and benthification (Bezerra et al. 2018).

In floodplains, the pulse decreases the spatial variability (Thomaz et al. 2007) and affects the biological composition (Emiliani 1997, Agostinho et al. 2004); consistency – biomass; ecosystem processes (Angelini and Agostinho 2005); ecological preferences – resource partitioning (Correa and Winemiller 2014) and interactions (Abujanra et al. 2009, Chaparro et al. 2015); and size - individual weight (Angelini et al. 2006). In the Paraná river floodplain, food is a limiting factor for low trophic levels in dry periods (Esteves and Galetti 1995), when predation rates are higher (Luz-Agostinho et al. 2009) and the low turbidity is associated to the higher productivity (Abujanra et al. 2009). Still, the Primary Production (PP) increases as a consequence of an increase in the allochthonous food intake during the floods (Junk et al. 1989), when the probability of biotic interactions are lowered (Lima et al. 2012, Padial et al. 2014). Therefore, the way by which bottom-up forces and the raising PP influence trophic interactions is still controversial (Abujanra et al. 2009, Correa and Winemiller 2014, Marchese et al. 2014).

In the first chapter, we revisited the fish biodiversity in the Paraná river floodplain by aggregating biodiversity (biomass, size, and density, “BSD approach”) in functional groups related to feeding-habit, trophic level (TL), and origin (native vs. non-native). Nevertheless, few common species still hindered the dynamics of rare species. Here, we represented the life history of fish species according to the size variation and to an external influence (water level) to model the ecosystem dynamics of functional groups. We used a food web approach to investigate a series of hypothesis, that are:

- if the flood pulse controlled the biomass of functional groups in the Paraná river floodplain;
- if the flood-control benefited non-native benthopelagic and demersal species more than native pelagic;

- If environmental changes observed and connected to the flood-control can explain long-term changes in the fish community in terms of size, composition, trophic level, and habit.

We expected answers at the ecosystem level, and dynamics resulting from the trophic interaction between functional groups. With such hypothesis, we also expected the functional groups, the origin, and the surrounding environment as central proxies of biodiversity.

Methods

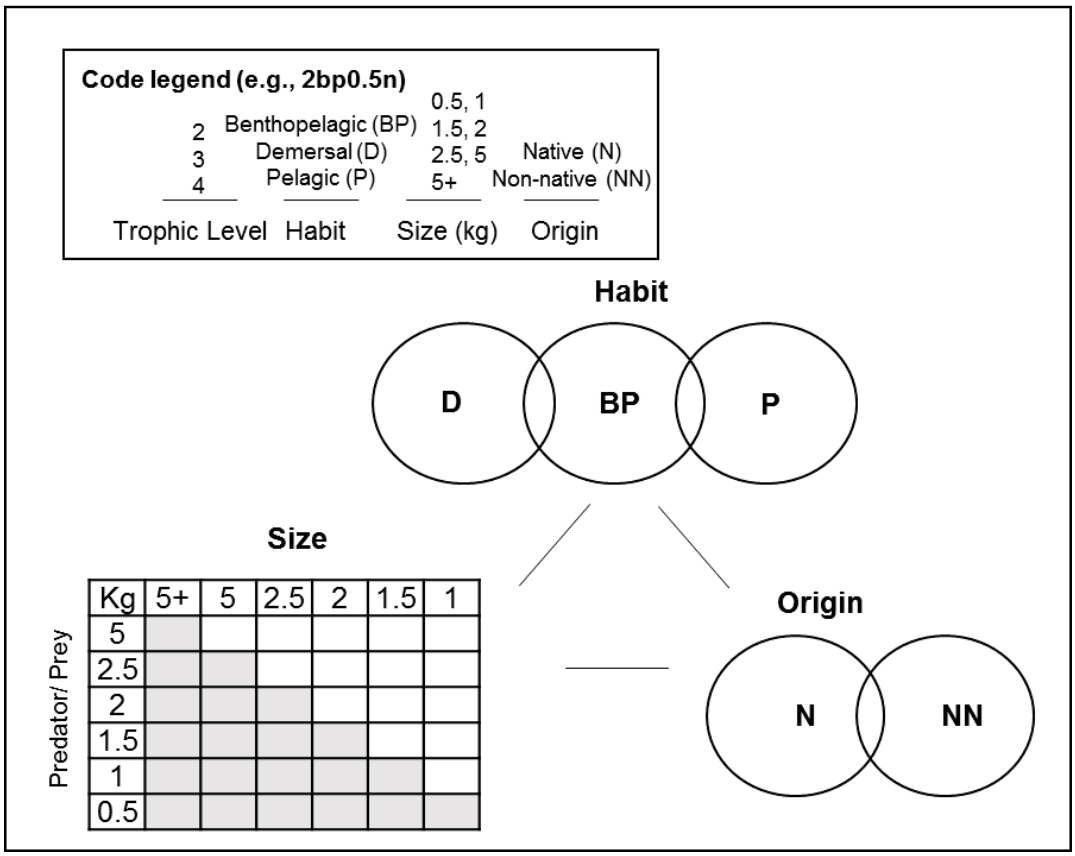
Dataset and the theoretical approach

We used the data from the Long-Term Ecological Program from the Universidade Federal de Maringá (PELD-UEM), in the Paraná river floodplain, that monitored seasonally fish species with nets and seines, from 2000 to 2017. Sampling methods that generated our databases were detailed in recent works (Ceschin et al. 2018), as well as in <peld.uem.br>.

We aggregated fish species according to their habit (benthopelagic, demersal, and pelagic), origin (native and non-native), and trophic level (TL2 to TL4) in functional groups (please, see the Methods section and SM of the chapter I for further details). Each functional group was later segregated by size, obtained from the log-scale distribution of weights (Figure SM1). Such distribution generated seven size-classes: 0-0.5kg (labelled as 0.5), 0.51-1kg (1), 1.1g-1.5kg (1.5), 1.51-2kg (2), 2.1-2.5kg (2.5), 2.51kg-5kg (5), higher than 5kg (5+). For instance, TL2-benthopelagic (2bp), sizing 0.5 kg, and native (2bp0.5n). Therefore, such representation incorporated the life history of a species in long-term as way to decrease the determinism of mass-balance approaches, which are also species specific in most of the studies (Colléter et al. 2015).

Our approach was a mixture of size-based and food web models, depending on the habit and origin of functional groups. We organized the diet matrix as a logical structure in which benthopelagic and top- predators were generalists (Square 1). Demersal and pel did not interact by predation and neither fish of the same size.

Square 1. Model structuring (size-based food web)



Among the models available in literature (e.g., Atlantis, Osmose, EwE), we have chosen the EwE approach (Christensen and Walters 2004) because it offered the flexibility to represent fish behaviour (ecological relevance as state variables) and multi-stanzas (age or size classes) in functional groups (Steenbeek et al. 2016). Although other tools (and in particular Osmose) might be able to incorporate these factors, EwE had the advantage of a rapid application and parametrization thanks to the large set of available information (Colléter et al. 2015) and capabilities to represent flexible diet matrix depending on size, habit, and trophic levels (Pinnegar et al. 2014). The peculiar representation of diet also facilitated the randomization of prey's vulnerability to predation, such as expected in the foraging arena theory (Ahrens et al. 2012).

The biomass (g.m-2) of functional groups was the sum of their weight per effort per sampling. In each season, the effort of gillnets was 1000 m2.day-1, which we added to the average effort by seines. The effort by seines decreased since the beginning of the historical series (Figure SM2), all seining averaging 205.98 m2. Since we measured the biomass, such decrease did not affect our

prediction beyond the sampling effect. Finally, we averaged the biomass of functional groups, yearly, from 2000 to 2017 to build our time series.

Modelling approach

We used an EwE model to represent static (Ecopath) and time- dynamic (Ecosim) scenarios. Such as previously discussed, the input data represented a size-based structure of functional groups tests against the sampled biomass of fish species. We fitted mortality and age (in months) to the biomass of each group, following the assumptions of a von Bertalanffy growth function (VBGF) and a stable age-size distribution (Christensen et al. 2008). We compared the mean mortality and consumption of the stanzas with published PB and QB (Froese and Pauly 2016), from which we also obtained the VBGF curvature parameter k (Table SM1).

Then, we simulated biomass variation of each functional group in the Ecosim for the following 17 years (period 2000-2017). The Ecosim equation for consumers, producers, and for non-living groups is broadly described in the literature (e.g. Celić et al. 2018). We did the mass-balance by fitting the modelled TL with the TL of the functional groups, available in Froese and Pauly (2016). While fitting the TL, we also observed that higher sizes should be always represented by higher TL.

Model parametrization and setting

We fitted the model with a time series with the relative biomass of the compartments. We used the relative biomasses of each functional group in the period as our time series into the Ecosim module of the EwE. We used a forcing function (FF) proportional the water level of the river (Figure SM3) to represent the dynamics of the Paraná river during the period of simulation, based in the flood pulse concept (Junk et al. 1989). Then, we divided FF for a constant (the first value registered in the series) that placed the variation around one. Finally, we applied the FF to the primary production rate. We did not simulate fisheries since the fishing pressure (number of boats and fishermen) didn’t change significantly in the period. We did all the following procedures after applying FF to the model, such as predicted in the flood pulse concept (Junk et al. 1989).

We used the routine “Fit to time series” of the Ecosim to achieve the best fitting in the period (Table 1). Generally, the sum of squares (SS) converged with less than 17 iterations. We re-ran the matrix using different sets of vulnerability, which is analogous to the availability of a given prey I to a predator j (Ahrens et al. 2012). We have chosen the best model the one with the lowest SS. Finally, we saved the vulnerabilities resulting from the best model to proceed to the test of hypothesis.

Table 1. Model selection procedure, according to the number of parameters randomized (N) and 751 AIC data points (sample size). Reference SS = 1503.71. Vulnerabilities (V). Number of iterations (Ni).

N	SS	Ni	AIC	Observations
73	371.12	11	-367.4	Searched with time series & Sensivity of SS to V by predator, only non-fish prey
73	374.92	16	-359.75	Searched with time series & Sensivity of SS to V by predator
30	436.2	15	-345.4	Sensivity of SS to V by predator
30	466.6	16	-294.87	Sensivity of SS to V by predator, only non-fish prey
29	551.2	15	-171.9	Sensivity of SS to V by predator and prey, only non-fish prey
30	556.5	18	-162.6	Sensivity of SS to V by predator and prey
73	644.6	20	47.22	Searched with time series
73	645.6	20	48.36	Searched with time series, only non-fish prey
68	658	20	50.47	Searched with time series only for interactions with TL2 predators
48	1032.8	20	341.98	Searched with time series only for interactions with TL3 prey and TL2 predators
35	1355.25	20	516.86	Searched with time series only for interactions with TL3 predators

From the chapter I of this thesis, we observed an increase in the abundance of natives, non-natives, and TL2, depending on their habit. We increased or decreased deterministically the vulnerability to predation of the functional groups 20 times in relation to the initial value (Figure SM3) to observe the parsimony of each scenario at the ecosystem level, according to the SS resulting from the expected and predicted data.

Results

We registered 86 functional groups, 74 fish and 12 non-fish, from 2000 to 2017 in the Paraná river floodplain, including detritus, PP, and suspended organic matter (SOM). Basic estimates of the static module (the mass-balance of Ecopath) were represented in the Supplementary Material (Table SM1).

In the time-dynamic module (Ecosim), the best model fitted the biomass after forcing the biomasses with the water level (Figures 1 to 3). The FF on PP

preceded the variation of detritus, non-fish, and fish compartments, therefore, controlling the dynamics from the bottom. The higher availability of PP during strong floods (years 2007, 2010, 2011, and 2016) benefited more benpel in the TL2 (Figure 1) than dem and pel, particularly meso-predators of low-size (until 1 kg in TL2 and TL3), that controlled the consumption of higher trophic levels.

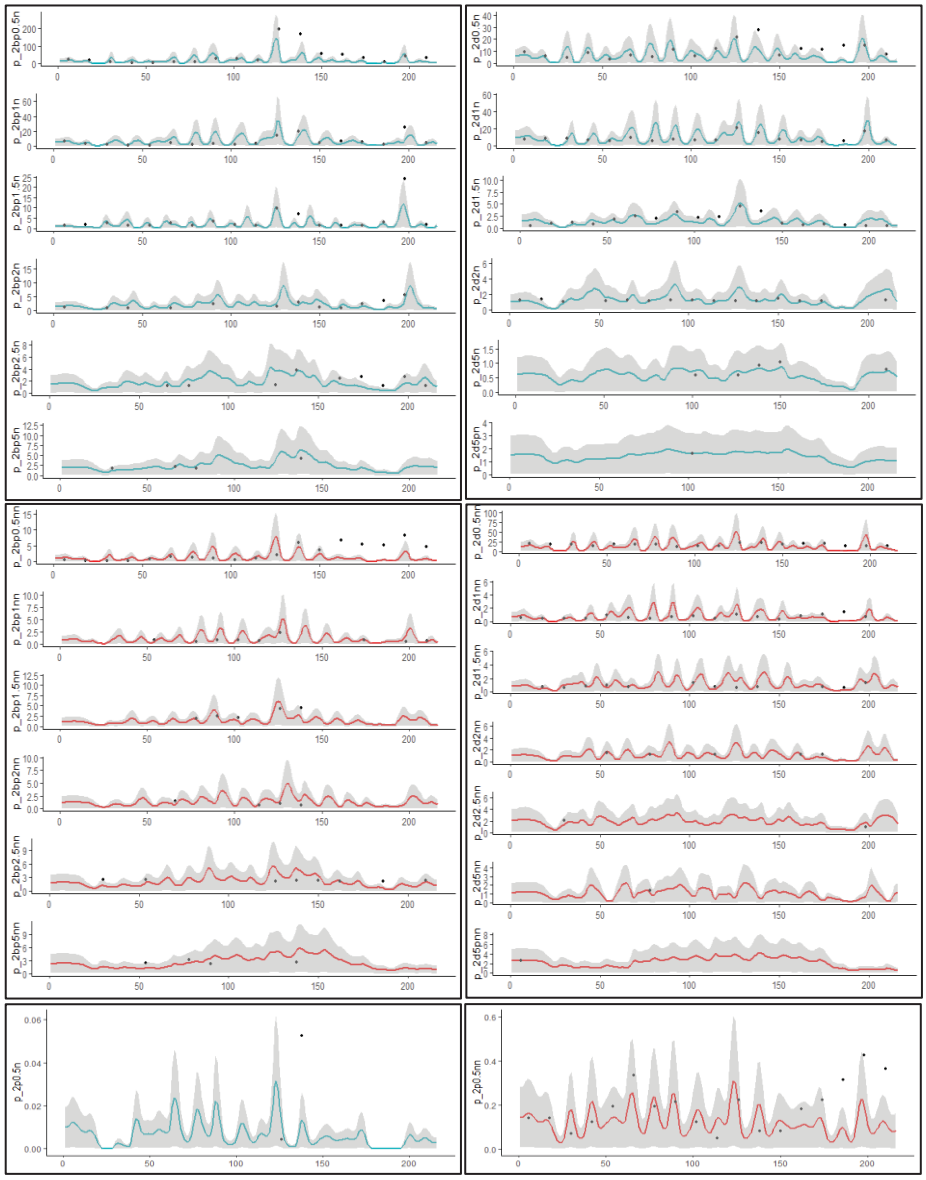


Figure 1. Relative biomass of functional groups (see the Methods section for further details) of the TL2, in the Paraná river floodplain. The full- lines (blue for natives and red for non-natives) represent the expected values, between 95% confidence intervals. Dots represent the measured biomass ($g.m^{-2}$), monthly, from 2000 to 2017 (216 time-steps, x-axis).

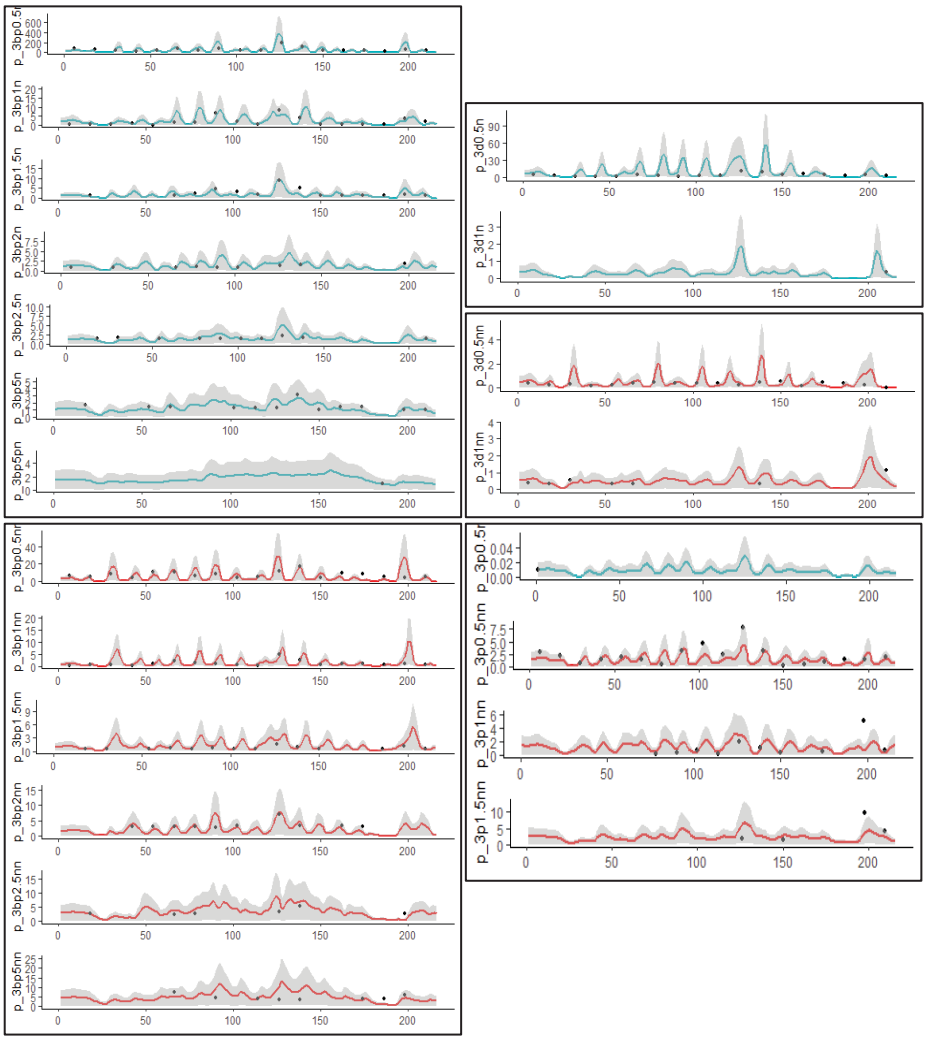


Figure 2. Relative biomass of functional groups (see the Methods section for further details) of the TL3, in the Paraná river floodplain. The full- lines (blue for natives and red for non-natives) represent the expected values, between 95% confidence intervals. Dots represent the measured biomass ($g.m^{-2}$), monthly, from 2000 to 2017 (216 time-steps, x-axis).

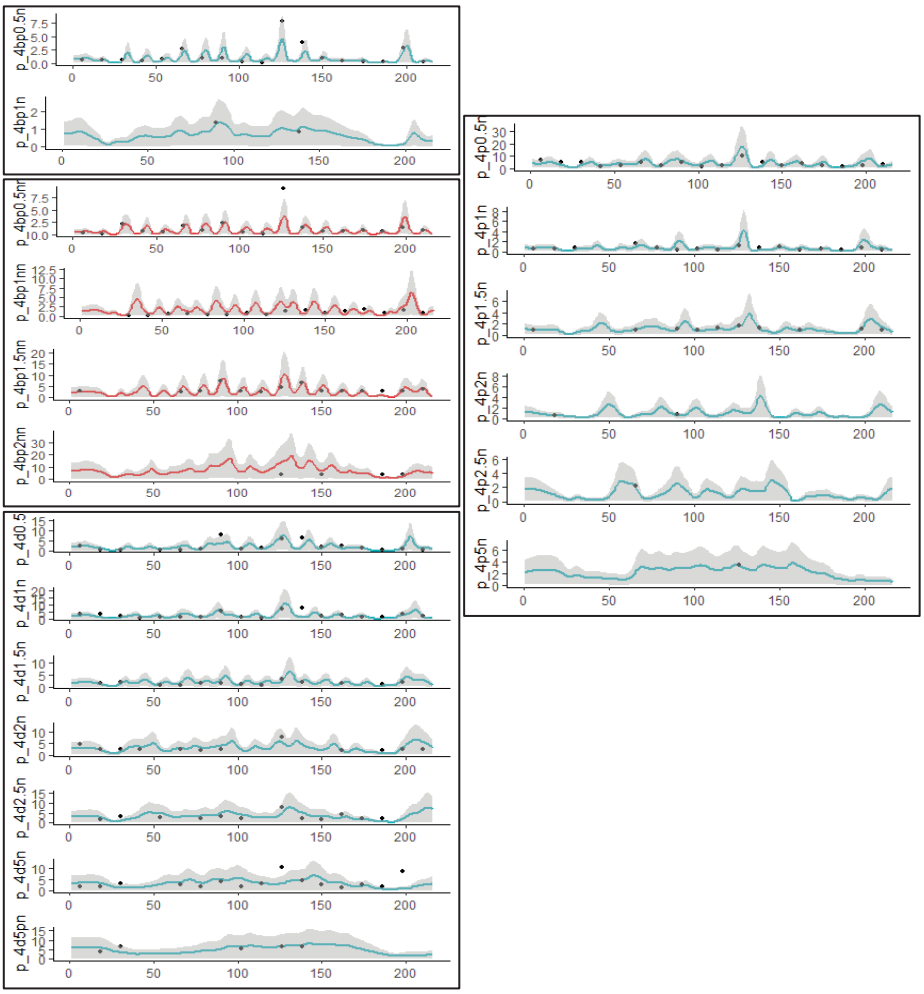


Figure 3. Relative biomass of functional groups (see the Methods section for further details) of the TL4, in the Paraná river floodplain. The full- lines (blue for natives and red for non-natives) represent the expected values, between 95% confidence intervals. Dots represent the measured biomass ($g.m^{-2}$), monthly, from 2000 to 2017 (216 time-steps, x-axis).

However, the model did not capture the expected dynamics of some non-native predators (2d0.5nn and 3bp5nn). Also, little non-natives with benthopelagic and pelagic habits had biomasses higher than expected by the model in recent years (2bp0.5nn, 2p0.5nn). Top predators and pelagic fish controlled the size-based structure from the top, which resembled a mixed-control in our modelling approach.

Pelagic species were key in the best scenario, as well as in the test of hypothesis. A decreasing vulnerability of pelagic species to predation resulted in the most parsimonious (lowest SS) scenario, in the time-dynamic simulation

(Table 2). Indeed, the next SS value reflected an increasing vulnerability of pelagic groups (mostly in the TL4).

Table 2. Test of hypothesis based in the Sum of Squares (SS), 751 AIC data points (sample size), and 72 parameters. Reference SS = 371.12.

SS	Observations
371.2	Decreasing vulnerability of pelagic
378.1	Increasing vulnerability of pelagic
380.2	Decreasing vulnerability of TL2
409	Decreasing vulnerability of native
416.7	Increasing vulnerability of TL2
424	Increasing vulnerability of native
428.7	Decreasing vulnerability of demersal
442.3	Decreasing vulnerability of TL4
443.5	Decreasing vulnerability of benthopelagic
445.2	Increasing vulnerability of TL4
470.5	Increasing vulnerability of demersal
475.6	Decreasing vulnerability of non-native
501.2	Increasing vulnerability of benthopelagic
525.3	Decreasing vulnerability of TL3
582.3	Increasing vulnerability of non-native
599.6	Increasing vulnerability of TL3

Discussion

Flood pulses controlled the biomass of functional groups when altering the Primary Production (PP), which reinforce the structuring power of bottom-up forces in the food web of the Paraná river floodplain (Pendleton et al. 2015). The fluctuation of PP and detritus generated a huge increase in the biomass of low and intermediate consumers, which benefited higher trophic levels, but no necessarily during the flood period. As the water level increase, beta diversity decreases with the spatial homogenization of the environment (Ceschin et al. 2018), followed by the allochthonous input and by the increasing abundance of phytoplankton (Rodríguez et al. 2011) and periphyton (Carapunarla et al. 2014) adhered do macrophytes, which decreases the limiting power of predation (Abujanra et al. 2009, Luz-Agostinho et al. 2009), and reveal the importance of the flooding as an environmental filter of the fish biomass in low TL.

Later, in dry periods, pelagic piscivores find a higher availability of biomass of fish that benefited previously of the flood. Such alternative states benefit respectively piscivores and benthopelagic fish. Therefore, It complements

previous studies that revealed a lower body condition of piscivores during the flood (Luz-Agostinho et al. 2009). However, apart from the individual behaviour, our findings suggest that the alternative states linked to the flood pulse are better understood at the ecosystem level.

Functional groups from phytoplankton to fish can answer differentially to the water level variation (Padial et al. 2012, Marchese et al. 2014). By increasing the foraging arena (Ahrens et al. 2012), the water level also influence the feeding behaviour of piscivore species (Luz-Agostinho et al. 2009, Pereira et al. 2017). It was represented in our approach by the size structure (big individuals feeding on little) and by the bottom-up control of little (0.5 kg) pelagic and benthopelagic in low trophic levels, which means that:

1) in complex systems like riverine floodplains, pelagic species can follow the optimum foraging theory as far as they find alternative states, the flooding (when youngers benthopelagic and demersal preys arise), and the low water, when piscivores prosper. Alternatively, piranhas (*Serrassalmus* spp.) and trahiras (e.g., Hoplias spp.) are highly opportunistic pelagic and benthopelagic predators since their early life-stages. Even if their biomass does not follow the flood pulse (Luz-Agostinho et al. 2009), they are benefiting from bottom- up forces triggered by alternative states of the flood pulse and increasing in biomass in the floodplain (Pendleton et al. 2015, Pereira et al. 2017).

2) oligotrophication and benthification are limiting the predation in the Paraná river floodplain only indirectly. Detritus remains a black box, but it is clearly an alternative food source to the food web, especially during the floods. Most of the bottom-feeding species were in the TL2 and in the TL3, so that the success of such meso-predators was also related to the detritus cycling in the ecosystem. Scientists highlight the role of detritus cycling abroad (Fish and Carpenter 1982, Gubiani et al. 2011, Winemiller et al. 2011, Deehr et al. 2014). In the Paraná river floodplain, the consumption of benpel and dem species increased the availability of energy to top predators (including pel), such as expected before by other authors (Chaparro et al. 2015). Nevertheless, we could not assure if detritivory was a cause or a consequence of the domination by intermediate predators in flood periods.

3) non-natives are evolving rapid advantages in relation to the native biota, corresponding to a fast establishment in the invaded environment. Even so, non-

native predators, especially demersal in TL4 (e.g., hybrid pintado) were sensitive to meso-predators, that increased in abundance in the modelled period (such as observed in the chapter I). Non-native preys in TL2 benefited native and non-native predators, however, prey's observed biomass was higher than expected by the model, and the predation pressure over them seems not so strong to the point of decreasing their biomass.

On other hand, the fact that both decreasing and increasing vulnerabilities of pelagic were parsimonious means that interactions with this keystone group limited the food web both from the top and from the bottom. Indeed, three of the lowest SS values were native, pelagic, and TL2, which was also observed in the Chapter I. Therefore, it suggests a mechanism through which such groups are increasing in biomass due to less vulnerability to predation. In fact, this kind of mixed- control is not uncommon in aquatic ecosystems (Angelini et al. 2011).

Here, we brought together a simple way to represent biodiversity, based in abundance and in the life history of functional groups, trophic interactions, and the influence of environmental filters. We believe to have contributed to the conservation of functional groups in the Paraná river floodplain while revealing that the system can be strongly based on predation, considering long-term changes associated to the water level of the river. Indeed, that the ontogeny (size variation) of top-predators and pelagic resembles an internal top-down control by big individuals on small size-classes but the most significant structuring force is the flood pulse. Such groups are homogenizing the biodiversity in fresh waters towards a size and trophic level, which restricts their ecological services and increases their vulnerability to non-native top-predators. However, the complexity of the Paraná river floodplain cannot be reduced to the patterns found here. Even if our model can serve as a proxy for other rivers and floodplains in neotropical regions, such as floodplains of Amazon, such rivers can be much more complex. However, we highlight that our approach is not focused in species, but on the ecosystem functioning, which is friendly to the management (Angelini and Agostinho 2005, Strayer 2012, Cooke et al. 2016).

We conclude that the water level, now controlled artificially by upstream reservoirs influence the functional biodiversity in the Paraná river floodplain while favouring the domination by intermediate groups, independently on their habit.

Such domination drives the ecosystem from the bottom, which determines partially the abundance of native groups. Otherwise, the meso-predators release can be an evolutive advantage for some non-native groups. Anyway, intermediate predators are the primary key to understand the dynamics of the ecosystem. Contrarily to trendy practices of decision makers, the management should also focus meso-predators (e.g., pelagic in TL2), since their size-structure, origin, and behaviour determine the environmental quality and the success of top-predators. Managers should monitor trophic interactions between broad groups (particularly, demersal and pelagic mesopredators), and their interaction with the surrounding environment, which includes the oriented management of non-natives (Pelicice and Agostinho 2009, Nobile et al. 2018), macrophytes (Chaparro et al. 2015, Ceschin et al. 2018), and detritus (Bezerra et al. 2018).

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CHAPTER III

Benthification, biotic homogenization behind the trophic downgrading in altered ecosystems

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Abstract

Several dozen fish species have been introduced into neotropical waters, causing significant biotic changes that include deterministic predation interactions with ecosystem effects. In general, reservoirs are preferred over lakes as places for stocking policies, due to their artificial aspect, consequently promoting fish introductions. In a metanalytic approach, we compared the biomass of plankton-feeding (and top-predators) with bottom-feeding fish species between reservoirs and lakes, considering the influence of invaders and trophic levels. Among the 26 ecosystems (12 reservoirs and 14 lakes), there is a dominance of non-native bottom-feeding species in artificial environments. We revealed a mechanism behind this dominance in a study case, a tendency for trophic downgrading and biotic homogenization based on interactions between an expatriate invasive centrarchid (sunfish family) predator from North America (the largemouth bass Micropterus salmoides) and two omnivorous cichlids from Africa in novel environmental contexts in Brazil (the “benthification” process). Both juvenile and adult largemouth bass are keystone predators in aquatic food webs in both their native and introduced ranges. The omnivore-detritivore tilapiines Oreochromis spp. and the phytophagous-omnivorous Coptodon spp. are species that exhibits strong generalist tendencies. Such species feed on the omnivore and detritivore compartments, enhancing detritus cycling among a large variety of δ13C sources. Since their consumption is disproportionate, facilitation of other species occurs with multiplicative effects in the environment. Interactions between invasive species, i.e., when an invasive predator (bird, fish, or invertebrate) eats an invasive prey (mainly fish and invertebrates), can serve to highlight biotic homogenization on fresh waters.

Keywords: Invasional meltdown; predation interactions; stable isotope; energy flow; food web modeling, Ecopath with Ecosim, downgrading food webs, trophic homogenization.

Introduction

Large-scale environmental alterations such as climate change (Blois et al. 2013), impoundments in aquatic ecosystems (Rahel 2007, Johnson et al. 2008), and introduction of non-natives (Leprieur et al. 2008, Vitule et al. 2015) increased the likelihood of biotic homogenization in the Anthropocene (McKinney and Lockwood 1999, Magurran et al. 2015). More than half of the dammed basins in the world host at least one non-native fish species (those introduced in artificial or natural environments outside their native range), while non-natives represent more than a quarter of the fish species richness when six hotspots of invasion are considered (Leprieur et al. 2008). Not surprisingly, the highest proportion of native and endemic fish species listed on the IUCN Red List occur in dammed riverine basins (Leprieur et al. 2008).

Expansionist policies from the early 1970s until the end of the 20th century anticipated the construction of thousands of reservoirs in developing economies, with a focus on hydroelectric power and water storage. Such policies modified most of the riverine basins in the world (Agostinho et al. 2016, Winemiller et al. 2016), and a demand for new inland fisheries has resulted in programs for the introduction of lentic-pre-adapted native and non-native species to reservoirs (Rahel 2007). On average, 85% of the Neotropical reservoirs host less than 40 species (Agostinho et al. 2016) adapted to lentic conditions and in some degree dependent on nutrient accumulation and recycling, much of them non-native (Rahel 2007, Johnson et al. 2008, 2009, Gallardo et al. 2016). Such species have been introduced for commercial and sports fisheries, and for aquaculture (Britton and Orsi 2012, Winemiller et al. 2016). When introduced into reservoirs, as opposed to natural water bodies, non-natives are likely to find themselves amongst an impoverished assemblage of native species, a factor that facilitates the invasion process (Johnson et al. 2008, Petesse and Petrere 2012). Alien invaders in reservoirs exhibit all three of the notable aspects of biological invasion: “population spread, community dominance, and range expansion” (Gurevitch et al. 2011). Multiple invaders are likely in this kind of environment,

and their interactions, as well as their influence over the native biota, are not fully understood (Britton and Orsi 2012, Simberloff and Vitule 2014). Therefore, reservoirs are among the best places to observe human-induced effects (damming and the introduction of non-natives) over the natural fish biodiversity (Agostinho et al. 2016, Winemiller et al. 2016). The introduction of largemouth bass (Micropterus salmoides) and tilapiine cichlids of the genera Oreochromis are commons examples of species introduced worldwide for human purposes, ranking them among the top 100 of the world's worst global invaders (Lowe et al. 2000), and interacting by predation in their habitats.

The secondary invasion is a kind of facilitation with mutual benefits for both or at least for one of the interacting species that encompasses a broad range of biotic and abiotic phenomena (Pearson et al. 2018), which include predation of invader species by another invaders, if there is an ecosystem effect (O'Loughlin and Green, 2017). If prey's fitness increases with a decrease in the intraguild competition, the predation interaction creates benefits to both prey and predator (Bezerra et al. 2018). Multiple interactions among invaders at different trophic levels could precipitate or accelerate biotic homogenization through cascading effects (Olden et al. 2004, Bwanika et al. 2006, Rahel 2007, Johnson et al. 2008, Preston et al. 2012), which can cause a complete and irreversible shift in the species assemblage by increasing the likelihood of additional invasions (Simberloff and Holle 1999, Simberloff and Vitule 2014, Bezerra et al. 2018). Food web models in aquatic environments indicate a large dependence on detritivores and pelagic filter-feeders to sustain upper trophic levels dominated by predatory fishes (Liu et al. 2007). Bottom-feeding species, mainly non-natives, lower the degree by which predators and plankton-feeding species could limit the consumption – the "benthification" (Mills et al. 2003, Mayer et al. 2014) process – biological invasions and ecosystem alterations towards the dominance of bottom-feeding species and trophic downgrading.

Here, we investigated the ongoing dominance of bottom-feeding species in altered ecosystems (reservoirs) in relation to natural lakes. Specifically, if this dominance was linked to the presence of non-native species, based on the benthification hypothesis. To this aim, we followed three approaches: (a) An analysis of meta-data for a comparison of 26 environments (12 reservoirs and 14 lakes) under differential influence of non-native species; (b) A trophic web model

for an artificial environment in Brazil (Passaúna reservoir) to represent interactions between natives and non-natives, and its effects; (c) A calibration of this model with stable isotope analysis from the same environment, illustrating how fish invasions could result in a class of non-native predator-prey novel interaction powered by a destabilizing positive feedback loop at the ecosystem level.

Therefore, if reservoirs are preferred for introductions, particularly of non-native fish (Rahel 2007, Agostinho et al. 2016, Winemiller et al. 2016), and if bottom-feeding fish have prospered in reservoirs, the success of non-natives and bottom-feeding fish could be related in some degree. In fact, non-native fish biomass or interactions should be (a) especially prevalent in reservoirs and scale-dependent (highlighting ecosystem level vs. species-based approaches) (b) more common with other non-natives than expected with native prey and predators, and (c) linked to the distribution of trophic levels, so that the dynamics of invaded, artificial systems can exhibit high stochasticity along with biotic homogenization.

Methods

Meta-data analytic approach

We examined the Ecobase (an electronic basis of Ecopath with Ecosim models, available in <http://sirs.agrocampus-ouest.fr/EcoBase>), in a search for biomasses of fish species that fed on benthic and pelagic sources (including benthopelagic, omnivore, and carnivore or plankton-feeding species) reported in food web models of lentic fresh waters (lake or reservoir). We complemented the search with a model developed to the Passaúna reservoir and Ecopath models published in electronic libraries (Web of Science and Google Scholar). We only examined peer-reviewed journals published in the English language. To avoid pseudoreplication, we classified all fish groups at once in one of the two habit categories (benthic-feeding *vs*. plankton-feeding). We searched the habit of all fish species, or in Froese and Pauly (2016) if the authors did no mention the habit. We considered one food web model per published paper (the most recent) and one effect per ecosystem (lakes or reservoirs). We also examined only ecosystems in which fisheries were allowed (except the Passaúna reservoir). If there were two or more periods for a single model, we always used the last, most recent, scenario. For instance, we examined Lake Victoria at once, in 2007.

Since total biomass variated a lot from one model to another (e.g., Lake Victoria *vs*. Passaúna reservoir), we standardized the fish biomass of bottom-feeding and plankton-feeding (or pelagic predators). We divided the biomass of each of these two groups by the mean biomass of all groups in the ecosystem (units given in $t.km^{-2}$ or $g.m^{-2}$). Standard deviation (sd) was not an input (equals to 0.5 to all groups). Therefore, the effect size (standard mean difference, SMD) and sd bars were all proportional to the raw difference in biomass between groups (PP minus BF).

In parallel, we classified the ecosystems with High (H), Intermediate (I), or Low (L) influence of non-natives. In H, non-natives dominated the fish community; in I, there was a similar composition of natives and non-natives and a reported ecosystem effect of the last; while in L, there were no or few non-natives without a reported effect. Finally, we joined habitat (lake or reservoir) and non-native influence (H, I, L) as a single predictor of the calculated effect sizes.

Study area

The Passaúna Reservoir (25º 31' 59.9" S; 049º 23' 16.5" W) is one among many reservoirs built in tropical regions for supplying fresh water for human use. The reservoir extends over 10 km^2 and is the primary water supply for Curitiba, one of the ten largest cities in Brazil with ~1.8 million inhabitants. It is relatively shallow, with a mean depth of 6.5 m, a hydraulic residence time of about 290 days, and classified as mesotrophic (Carneiro et al. 2016). However, it receives its water supply from small rivers in surrounding urban, agricultural and industrial areas, a situation that can push water bodies toward eutrophic conditions. Human activities are in keeping with their multiple uses, including irrigation, sports fishing, recreation and water storage (Carneiro et al. 2016). The region is in the C-climate zone and Cfb climate in Köppen's classification for Brazil, with a mean temperature of 17 ºC (see Alvares et al. 2013 for further details on the climate).

Fish and invertebrates: sampling and laboratory analyses

Fish were also sampled monthly from May 2011 to April 2012, in a combination of artificial baits and gillnets with panels ranging from 5 to 40 m in length, 1.3 to 5 m in height and a mesh size from 15 mm to 150 mm knot-to-knot. Gillnets (on

average nine sets per month) were set in randomly stratified locations and soaked for 24 hours. Sampling with artificial baits was carried out on 26 days, standardized with about eight hours of effort per day. Pelagic invertebrates were captured locally with plankton nets (500µm) or identified in the stomach contents of fishes and recorded just as mesozooplankton - MesZoo (Cladocera and Copepoda). Insecta was represented predominantly by *Martarega* sp. adults and *Chaoborus* sp. larvae.

We oriented the sampling to represent the (macro) biota in specific ranges, near to the dam barrier, and nearshore (with 6.5 m of mean depth), aiming to preserve fresh tissues for stable isotope analysis. Electrofishing was used to capture fishes and invertebrates in a specific area (nearshore and parallel to the dam) in a standard transect about 2 km in length, with each sample constituting 1.5 hours of effort. The electrofishing occurred monthly in cold - dry (April 2011 to October) and hot - wet (November 2011 to March 2012) periods. All fish specimens were identified to the lowest possible taxonomic level, measured (standard length, SL mm), and weighed (mass, ± 0.1 g) in the laboratory. We also examined the diet in the multivariate space, which tended to confirm the existence of three ontogenetic functional groups.

Because adult fish are more resistant to electrofishing than juveniles, we captured adult life stages of *M. salmoides* (Micsal) only with artificial baits - maximum length in capture (Lmax): 214 mm. Indeed, we used mainly nets to capture the native predatory characoid *Hoplias malabaricus* (Hopmal, Lmax: 520 mm). Even if both Lmax were lower than expected in the literature, 970 mm and 650 mm, respectively (Froese and Pauly 2016), Micsal was better represented by juveniles than Hopmal. Therefore, we classified the first into three life stages or “stanzas”: Juvenile 1 - J1 (smaller than 70 mm), Juvenile 2 - J2 (from 71 mm to 190 mm), and Adult - A (larger than 190 mm), while we placed the last only into two groups (juvenile - juv and adult), based on the asymptotic length – 1018.5 mm and 682.5 mm, respectively (Froese and Pauly 2016).

Beyond patterns in the capture, we divided species in stanzas for modeling purposes. We had differential information depending on species life stages, so that we set juvenile Micsal and adult Hopmal as “leading” the fit of other stanzas, in the “Multi-Stanza” routine of the Ecopath model (Christensen et al. 2008). We used this routine as an application of the Von-Bertalanffy Growth Function –

VBGF to approach the natural mortality - M of middle stanzas while retrieving M and consumption of leading stanzas from the published literature (Froese and Pauly 2016). We managed the VBFG growth parameter (k) for Micsal (from k = 0.3 to k = 0.9), in relation to Hopmal (k = 0.3), and fixed the time in each stanza (24 months) for both species. It brought realism to the simulation, taking our captures (representing a system with small Micsal and big Hopmal), and aligned with the literature, that reported a greater asymptotic length to Micsal.

On the trophic web modeling: The software Ecopath with Ecosim (EwE)

We used the EwE program and its plug-in Ecotroph (Christensen and Walters 2004a; Gascuel and Pauly 2009). In steady-state scenarios, the model predicts the production (*P*) of a prey *i* is from its predators *j* biomass (*B*), biomass accumulation (*BA*), consumption to biomass (*Q/B*) and production to biomass (*P/B*), assuming a fraction of the prey's *B* in the predator diet $(DC)_{ij}$ and an ecotrophic efficiency $(EE)_i$, estimated by EwE according to Equation 1.

$$\left(\frac{P}{B}\right)_i B_i = \sum_{i=1}^{n} \left(\frac{Q}{B}\right)_j B_j DC_{ij} + BA_j + \left(\frac{P}{B}\right)_i B_i(1 - EE_i) \quad \text{(Equation 1)}$$

We did not model other factors impacting the production of *i* such as migration and fisheries because our purpose was to emphasize predation interactions and because fisheries were prohibited in the Passaúna reservoir during the period of simulation. We showed specific modeling steps in the Supporting Information: "**Parametrization to the Ecopath modeling**". We identified stomach contents of *M. salmoides* (Micsal) to the lowest possible taxonomic level in the stereomicroscope while confirming identifications with specialists from "Capão da Imbúia" natural history museum in Curitiba, Brazil. First, we determined the biovolume of items in the stomach contents in graduated plates, then translating into percent representation by volume. We based the diet composition for *M. salmoides* on the stomach content of J1, J2, and adults. For diet information of the other components of the diet matrix, we consulted Froese and Pauly (2016) or specific references that investigated similar lentic and tropical reservoirs (Lazzaro 1991, Luiz et al. 1998, Deus and Petrere-Junior 2003, Delariva et al. 2013, Bezerra et al. 2018). We showed the general diet composition used as an input into the model in the supporting information (Table SM4).

Time-dynamic model: Ecosim

We represented the static model of EwE into a time-dynamic model (Ecosim, Christensen and Walters, 2004a). The start year on EwE met the date of sampling (mostly on 2011), variating in two scenarios, for the next 15 years: In the first (A), we increased the capture rate of tilapia linearly. In the second (B), we decreased the capture deterministically up to the point of collapse, i.e., biomass equals to zero (Figure SM4). The change in relative biomass of a prey *i* (dB_i/dt) varies according to the master equation of Ecosim (Equation 2):

$$\frac{dB_i}{dt} = g_i \sum Q_{ij} - \sum Q_{ij} + I_j - (MO_i + F_i + e_i)B_i \qquad \text{Equation 2}$$

In the equation, g_i is the net growth efficiency (production/consumption), Q_{ij} is the consumption of prey *i* by predator(s) *j* (that includes the vulnerabilities - V_{ij}), MO_i is the mortality due to other factors, F_i mortality due to fishing, and e_i and i_j the emigration and immigration rates, respectively, that not variates in time in closed systems. At low vulnerabilities ($V_{ij} < 2$), interactions are subject to strong bottom-up regulation. At higher vulnerabilities ($V_{ij} > 4$) the top-down pressures predominate (Christensen et al. 2008, Ahrens et al. 2012). Vulnerabilities were set randomly ($2 \leq V_{ij} \leq 4$) in a spreadsheet.

Parametrization to the trophic web modeling and uncertainty

The data used for the EwE analyses were biomass estimates of the community components along with their diets, estimates of the P/B and Q/B ratios, and literature-based data for ecotrophic efficiency. We used the routine “Ecoranger” (Christensen and Walters, 2004a) to re-sample from our input data (B, P/B, Q/B, EE, and diet), in 100 Monte-Carlo simulations (which could mean 100 different steady-states of the ecosystem) based on the Intervals of Confidence related to the quality of each introduced data (i.e., the model “Pedigree”, see **Table SM5**), then we used the best trial to force tilapia biomass in scenarios A and B.

We did this procedure to represent the stochasticity into our modeling. The pedigree index was an indicator of the degree to which native versus proxy data re-incorporated into Ecopath models (Christensen et al. 2008). We adapted the standard values (Christensen and Walters, 2004a), calculated as follows. Biomass values estimated from other models or based in the literature received a zero. Indirect methods, direct methods with low precision, and direct methods

with higher accuracy received scores of 0.4, 0.7, and 1, respectively — inputs of PB, QB, and diet in the standards (Christensen and Walters 2004a). Stomach analysis received 1 and literature-based data 0 in the pedigree index.

To improve the realism in our model, we included birds, known to make up part of the food web, from an inventory in the Sítios Novos reservoir, CE, Brazil (Bezerra et al. 2018). The geographic distance to the study area did not influence our simulation since we aimed to represent trophic interactions, and because all the included birds are common in Neotropical areas (Birdlife international initiative, <datazone.birdlife.org/home>). Birds were the cormorant *Phalacrocorax brasilianus*, Ardeidae, and “other birds” (uncommon but relevant groups, e.g., the kingfishers, halcyon, Alcedinidae: *Megaceryle torquata* and *Chloroceryle americana*). Except for some groups included in “other birds”, such bird species are found in freshwaters all over the world. Therefore, we presumed that its inclusion as consumers added reality to our modeling of a general scenario for reservoirs, beyond an incoming error associated with the sampling in the Passaúna. For the same reason, we grouped other fish compartments in “other piscivores”, “other insectivores”, “other invertivores”, “other omnivorous” and “other detritivores”. The biomasses in “other” compartments were retrieved from specific references, considering Neotropical reservoirs (Angelini et al. 2006, Gubiani et al. 2011, 2012).

Most of the fish compartments corresponded to individual species or functional groups so that we would be able to identify the role of non-natives in the food web. In addition to *M. salmoides*, we represented tilapias in a single compartment comprised of the genera *Coptodon*, *Oreochromis*, *Tilapia*, and their interspecific hybrids. We included the common carp (*Cyprinus carpio*) with “other omnivores”.

While selecting individuals of similar SL from the same collection site into composite samples before analysis, we removed a piece of white epaxial muscle tissue (ca. 20 mg dry weight) above the lateral line and below the dorsal fin. We identified the invertebrate samples to the genus level, later processed without subsamples. We dried sampled tissues at 60°C in a drying oven, then measuring carbon (C) and nitrogen (N) stable isotopic ratios on separate subsamples of the composite samples. We expressed isotopic values in delta (δ) notation (Coplen

2011). Replicate analyses of identical composites usually differed by ≤ 0.1‰ for both C and N stable isotopes.

The sample size for each isotopic determination was approximately 1 mg of δ^{13}C and 3 mg of δ^{15}N. We did not obtain isotopic values for J1 *M. salmoides* but from J2 individuals and adults (72 individuals). We conducted isotopic analyses at the Boston University Stable Isotope Laboratory (<www.bu.edu/sil/index.htm>). We did the flash combustion in tin boats at 1800°C in a Haraeus elemental analyzer, the separation of the resulting CO_2 and N_2 gases from the helium stream and cryogenic purification in a Finnigan cold trap, before introduction into a Finnigan Delta-S isotope ratio mass spectrometer. Finally, we measured against high-purity laboratory gas standards that we calibrated with international standards (Pee Dee Belemnite (PDB) for δ^{13}C and atmospheric air for δ^{15}N).

For detritus (microzooplankton, seston, and litter) and mesozooplankton (MesZoo), we retrieved δ^{13}C and δ^{15}N values from Reis et al. (2016). Stable isotope assessments were in line with steps of a model-oriented design, predicting biomass and diet composition for the main groups in the food web (Christensen and Walters 2004b).

Stable Isotope Analysis in R - SIAR (Parnell and Jackson 2013) was used to estimate the average contribution across trophic levels, with 95% confidence intervals. Basic estimates sampled from EwE included effective Trophic Levels (TL), non-integer TL *sensu* Odum (1969); Fdet - the contribution of detritus biomass to each of the modeled group; and the Omnivory index (OI), the variance on the TL of preys of *j*, that consider the diet fraction of preys *i* to consumers (*DCij*) (Christensen et al., 2008).

We first measured the effect of Isotope signatures on the food web (from community to the ecosystem). To do this, we used δ^{15}N and δ^{13}C as a proxy to the modeled TL, Fdet, and OI in General Linear Models (GLM) with “Poisson” distributions (pGLM), in three different models: TL or Fdet or OI ~ δ^{15}N and δ^{13}C. Then, we simulated the feedback of the ecosystem on the community (δ^{15}N or δ^{13}C ~ TL). We carried all analyses in R environment (R Core Team, 2017).

Results

We obtained 26 effect-sizes (12 reservoirs and 14 lakes), 23 negatives, while three positive tended to be in lakes or a reservoir with a low influence of non-natives (Fig. 1). The dominance of bottom-feeding fish occurred mainly in reservoirs with high influence of non-natives (R2 = 28.06 %; moderator HI effect (QM) = 12.9; P = 0.02). The biomass of bottom-feeding fish was commonly restricted to lower trophic levels (TL ≤ 3 or TL ≤ 3.5, if TL max ≥ 4), contrastingly with the biomass plankton-feeding species, generally with TL > 3 (or TL > 3.5, if TL max ≥ 4). However, the biomass of bottom-feeding was not always lower, with a large effect-size in lakes under intermediate influence non-natives (LI), this is, Annecy (France) and Lhema (Rwanda).

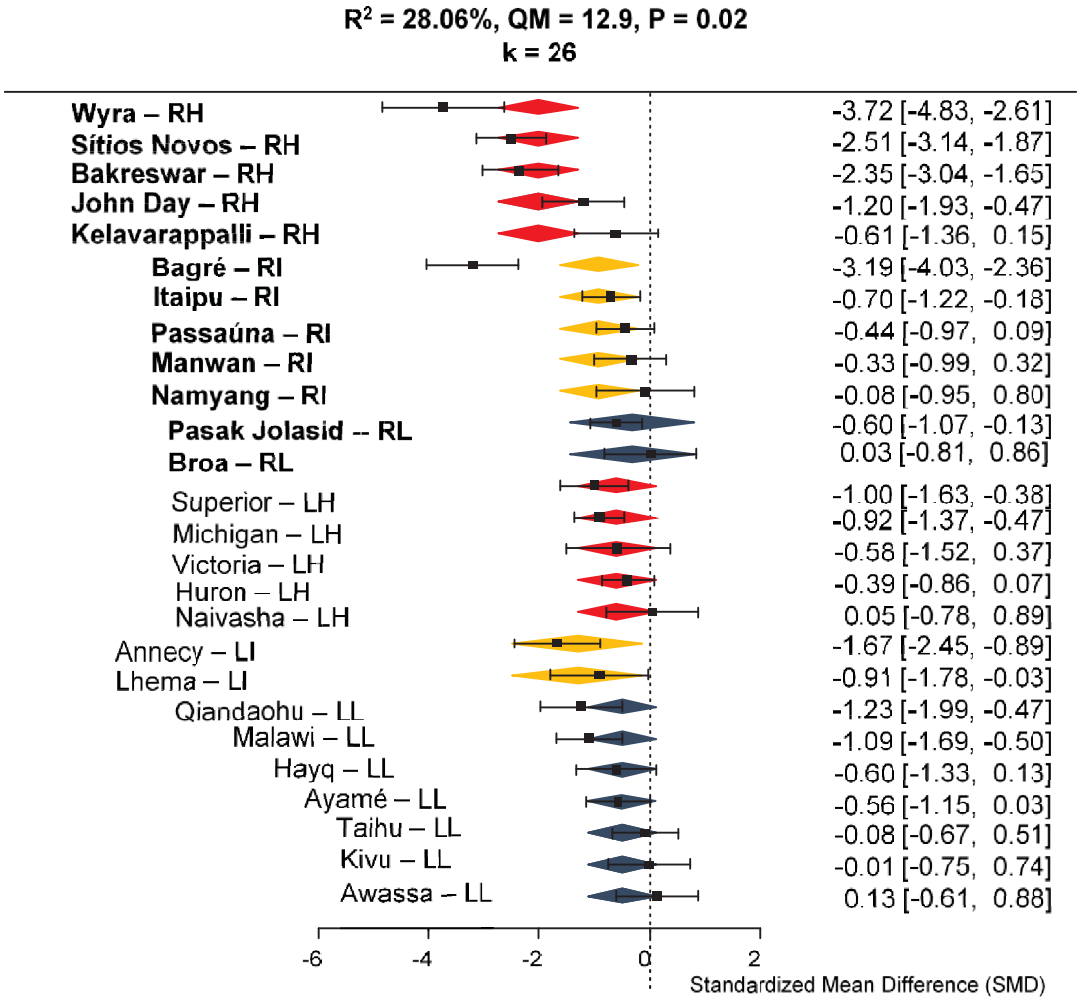

Figure 1 T Analysis of meta-data on the difference in biomass of pelagic predators and bottom-feeding species in reservoirs (R) or lakes (L), the first case letter in rows. The second letter indicates H – high; I – Intermediate, and L – Low influence

of non-native species. The influence H occurred when interacting non-natives dominated the fish community. On I, the community was composed equally by natives and non-natives with an ecosystem effect reported. On L, there were no or few non-natives without ecosystem effects. **Down**: Results of the mixed-effect model that we estimated with random effects and maximum likelihood (REML). Confidence Intervals (CI) at Low (Lo) and Upper (U) limits, Standard Error (S.E), and I^2 – residual heterogeneity / unaccounted variability.

Overall, we captured 1489 individuals, representing 20 species during the sampling program, and 28 compartments in the food web. The latter included 17 fish compartments, five invertebrates, three birds, two primary producers, and detritus (Figure 2). The native fish species were the large predator *Hoplias malabaricus* (a characoid), the herbivorous catfish *Hypostomus derbyi*, and the omnivorous *Geophagus brasiliensis* (cichlid), *Astyanax* spp. (characin), *Corydoras paleatus* and *Rhamdia quelen* (two more catfishes). Birds had the highest effective trophic level (TL 3.76), followed by *M. salmoides* A (TL 3.66), *M. salmoides* J2 (TL 3.62) and *H. malabaricus* adults (TL 3.59) and juveniles (TL 3.41). Top-predators had the highest accumulated biomasses, supported primarily by the biomass of fishes at intermediate trophic levels (from TL 2.57 – corresponding to *C. paleatus*, to *Astyanax* spp. – TL 2.857 and tilapia – TL 2.862). Detrital pathways contributed nearly twice the amount of assimilated food as primary production pathways.

Keystone groups in the ecosystem were *M. salmoides* adult and J2, *H. malabaricus* adult, and other piscivores, each with a Keystone Index (KI) greater than 1.0 and Relative Total Impact (RI) close to 1.0. We captured 105, 147, and 122 individuals of *M. salmoides* from categories J1, J2, and A, respectively. In the Ecosim, non-natives presented a differential response to the theoretical variation in the biomass of tilapia (in $g.m^{-2}.year^{-1}$), from 2011 to 2030. The native *H. malabaricus* biomass remained almost unaltered in the two scenarios (Figure 3A and 3B). A decrease in the biomass of tilapia decreased the *M. salmoides* biomass on 0.1 units (Figure 3A), but an exponential increase led to a decrease (Figure 3B).

Group	Name	ETL	B	PB	QB	EE	NE-GE	RA	RB
B	Ardeideae	3.82	1.66	0.26	1.71	0.329	0.04	0.81	1.11
B	*Phalacrocorax brasilianus*	3.69	0.04	0.11	0.77	0	0.04	0.82	0.51
F	*Micropterus salmoides* A	3.66	0.16	0.69	21.5	0.09	0.01	0.96	16.51
F	*Micropterus salmoides* J2	3.62	0.49	0.92	23.59	0.038	0.01	0.95	17.95
F	*Hoplias malabaricus* A	3.59	3.46	0.9	5.7	0.138	0.04	0.8	3.66
F	*Hoplias malabaricus* J	3.41	1.66	1.5	12.53	0.723	0.03	0.85	8.52
F	*Micropterus salmoides* J1	3.33	0.61	1.03	34.83	0.131	0.01	0.96	26.83
F	Other piscivorous	3.29	1.57	2.99	23.76	0.853	0.03	0.84	16.02
B	Other Birds	3.13	1.73	0.19	1.28	0.769	0.04	0.81	0.83
F	*Rhamdia quelen*	3.12	0.18	1.06	4.25	0.537	0.06	0.69	2.34
F	Other insectivorous	3.06	2.33	4.55	23.23	0.91	0.05	0.76	14.03
F	Tilapia	2.86	4.96	3.27	13.07	0.825	0.06	0.69	7.19
F	*Astyanax* spp.	2.86	1.04	11.75	47	0.756	0.06	0.69	25.85
F	*Geophagus brasiliensis*	2.85	1	2.13	8.53	0.894	0.06	0.69	4.69
F	Other invertivorous	2.65	2.26	2.16	20.2	0.982	0.03	0.87	14
F	Other omnivorous	2.64	2.56	6.23	39.47	0.748	0.04	0.8	25.35
F	*Corydoras paleatus*	2.57	1.25	1.78	16.52	0.9	0.07	0.82	8.13
F	Hypostomus derbyi	2.4	0.88	0.92	21.73	0.726	0.03	0.93	12.12
I	Insecta	2.27	13.68	10.09	40.36	0.9	0.06	0.69	22.2
F	Other detritivorous	2.23	2.31	5.29	44.72	0.922	0.03	0.85	30.49
I	Other Crustacea	2.16	12.7	22.5	90	0.498	0.06	0.69	49.5
I	Copepoda	2.11	8.88	24.18	96.70	0.161	0.06	0.69	53.19
F	Other herbivorous	2	2.96	8.16	29.26	0.799	0.07	0.65	15.25
I	Other Benthos	2	13.2	14.88	59.52	0.9	0.17	0.58	20.83
I	Cladocera	2	29.64	18.99	75.94	0.289	0.06	0.69	41.77
D	Detritus	1	23.75			0.452			
P	Periphyton	1	26.26	40		0.46			
P	Phytoplankton	1	31.66	183		0.29			

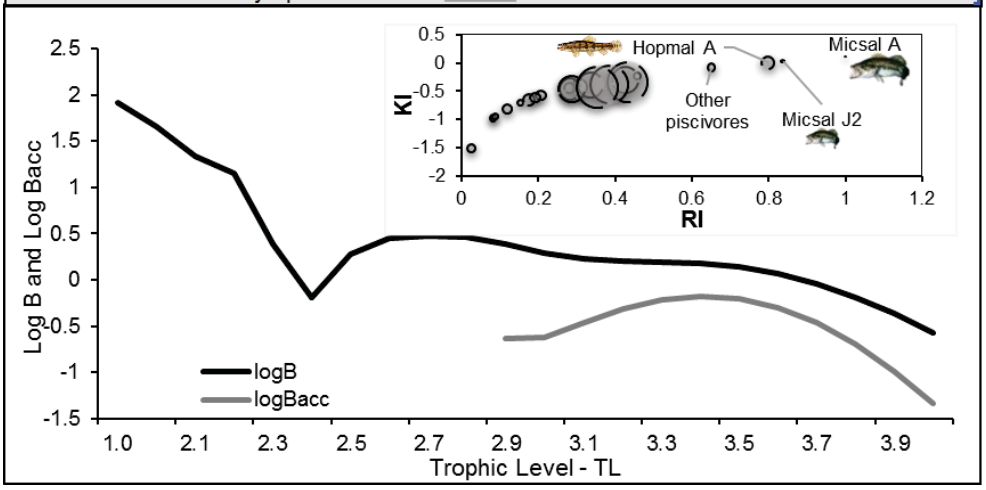

Figure 2. Top: Group identity (ID): B - Birds, D - Detritus, F - Fish, I - Invertebrates, P - Primary producers, and effective trophic level (TL); annual values of: biomass (B, scaled by bars), relative production (P/B), relative consumption (Q/B), Ecotrophic Efficiency (EE), Net Efficiency minus Gross Efficiency (NE-GE), Assimilation (RA) and Respiration/Biomass (RB). J - Juveniles 1 and 2 and A - adults. **Middle**: Keystone Index (KI) *vs*. Relative Total Impact (RI). Groups (28) scaled by biomass (bubble area). RI > 0.6 and KI > zero are identified. Hopmal – *Hoplias malabaricus*, Micsal - *Micropterus salmoides*. **Bottom**: Trophic spectra (*sensu* Gascuel and Pauly 2009) of log B and log Bacc *vs*. TL.

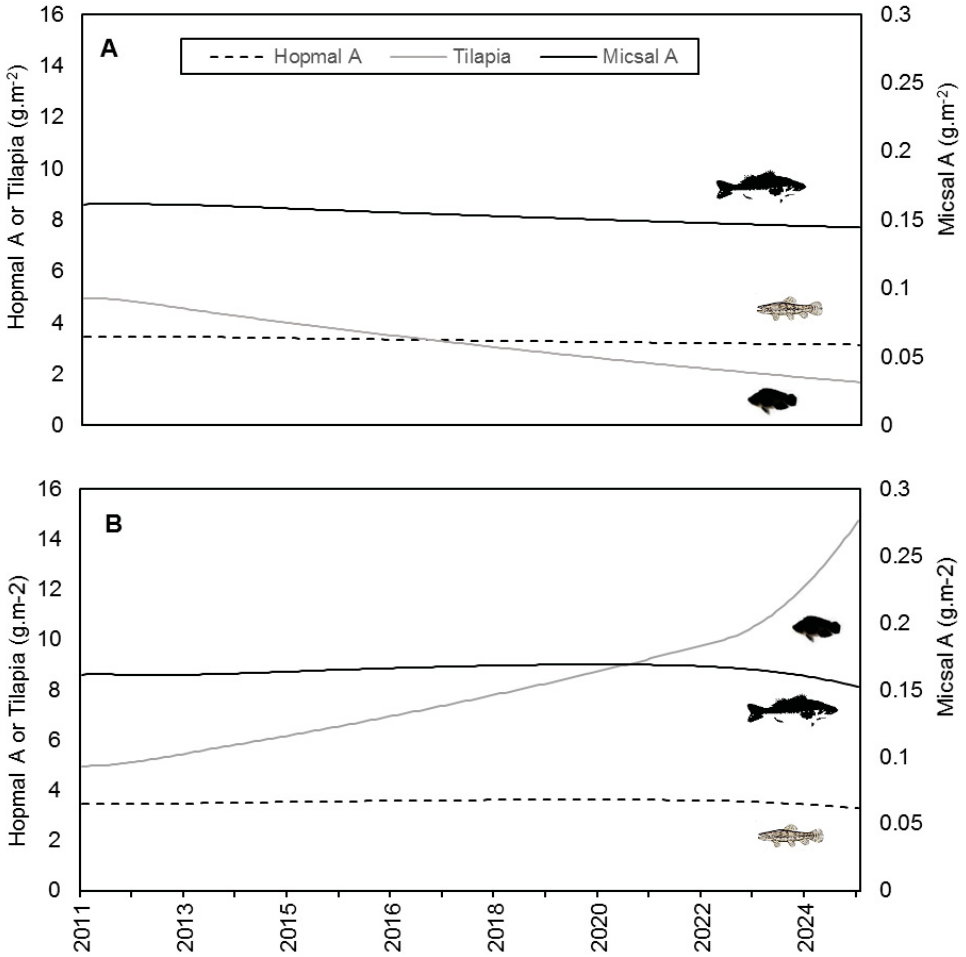

Figure 3. Ecosim model of the *Micropterus salmoides* adult (Micsal A), *Hoplias malabaricus* adult (Hopmal A) and tilapia, after Monte Carlo simulations on input values of the Ecopath model in the Passaúna reservoir, from 2011 to 2026. Scenarios are expressed with a deterministic increase **A** or decrease **B** in the capture of tilapia (see also Figure SM4).

The $\delta^{13}C$ and the $\delta^{15}N$ values of tilapia were more disperse than *M. salmoides* (juvenile and adult) and the native predator *H. malabaricus*, respectively **(**Figure 4). Carbon and nitrogen signatures variated with the ecosystem parameters TL and Fdet ($P < 0.05$), but not with OI (Figure 5). The consumption of $\delta^{13}C$ sources decreased with TL (Figure 5 A), while the $\delta^{15}N$ distribution increased, related to the consumption on detritus (Figure 5 B, C), independently on the richness of items in the diet of a given consumer.

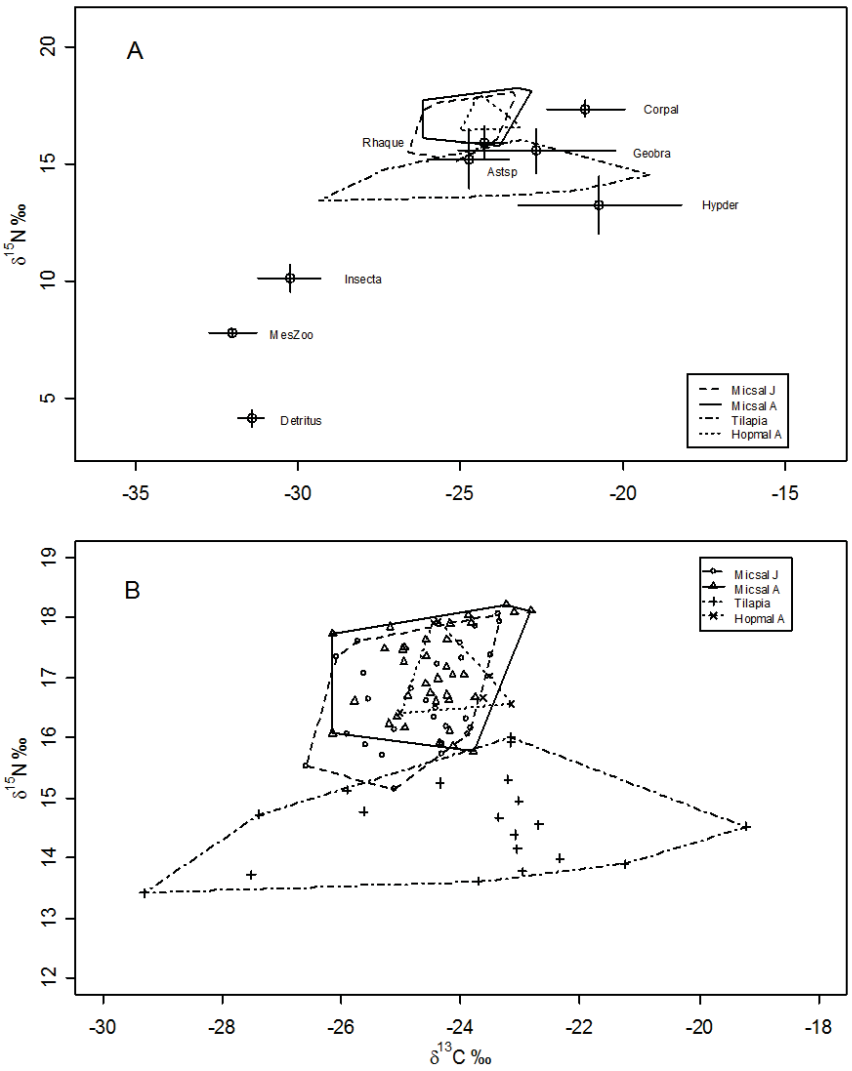

Figure 4. A Stable Isotope Analysis in R (SIAR) plot with standard deviance of isotope values for Astsp (*Astyanax* spp.), Corpal (*Corydoras paleatus*), Geobra (*Geophagus brasiliensis*), Hypder (*Hypostomus derbyi*), Hopmal A (*Hoplias malabaricus* adult), MesZoo (mesozooplankton, that are Cladocera and Copepoda), Micsal A (*Micropterus salmoides* adult), Micsal J (*Micropterus salmoides* juvenile 1 and 2), and Rhaque (*Rhamdia quelen*). **B** A close-up of **A** with Micsal A in solid lines and tilapia, Micsal J and Hopmal A in dashed lines.

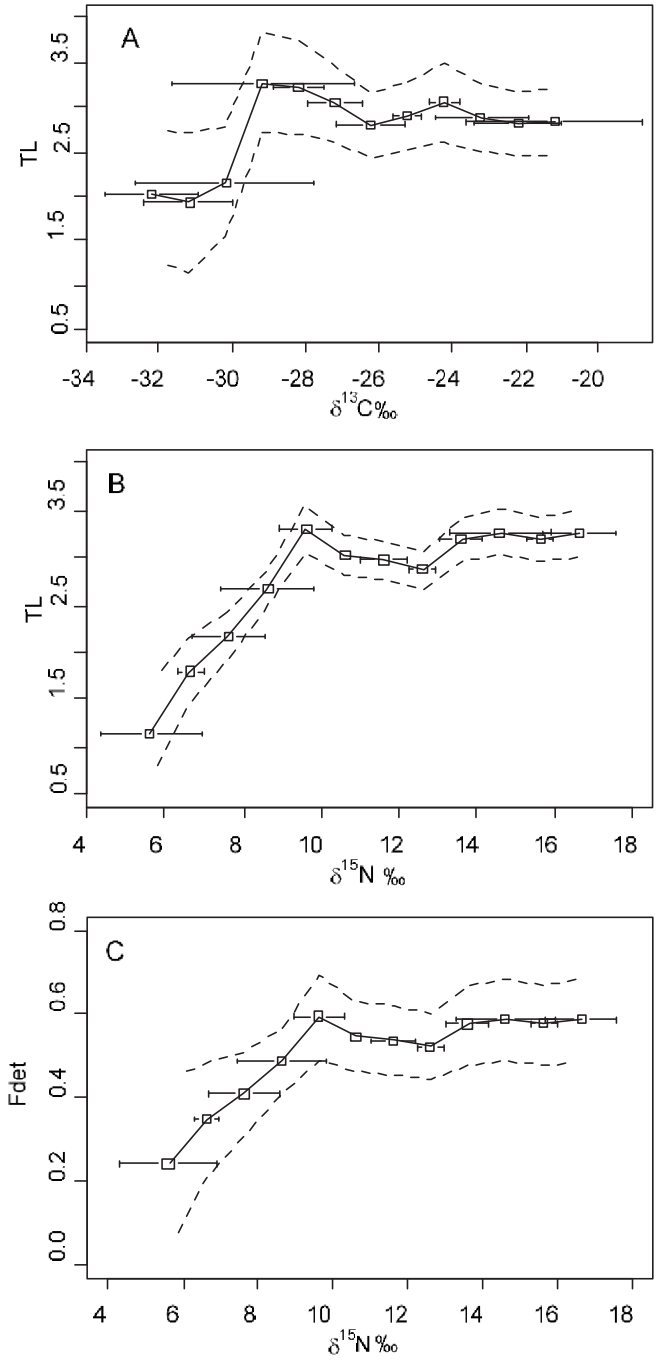

Figure 5. Modeled ecosystem variables and respective standard errors **A** Effective Trophic Level (TL), **B** Flow from detritus (Fdet), and **C** Omnivory Index (OI) according to the mean δ^{13}C and the mean δ^{15}N values in Poisson-distributed General Linear Models (pGLM). Only patterns ($P < 0.05$) are reported.

However, contrary to we expected from the modeled TL, mean δ^{13}C and mean δ^{15}N, values were highest for the benthic fishes *C*. *paleatus* and *H*. *derbyi*

(Figure 6). Increasing TL correlated positively with the mean δ^{15}N variation ($r_{spearman}$ = 0.76, P < 0.01), but not to the mean δ^{13}C variation ($r_{spearman}$ = 0.29, P = 0.35), while TL explained the isotopic variation of both δ^{15}N and δ^{13}C, unrevealing a feedback with redundant nitrogen food sources (Figure SM5). The only groups outside of the expected 95% confidence interval were the intermediate consumers *C. paleatus*, *H. derbyi*, and MesZoo. Indeed, the range of δ^{13}C isotope values for *H. derbyi* was the greatest among all the groups tested.

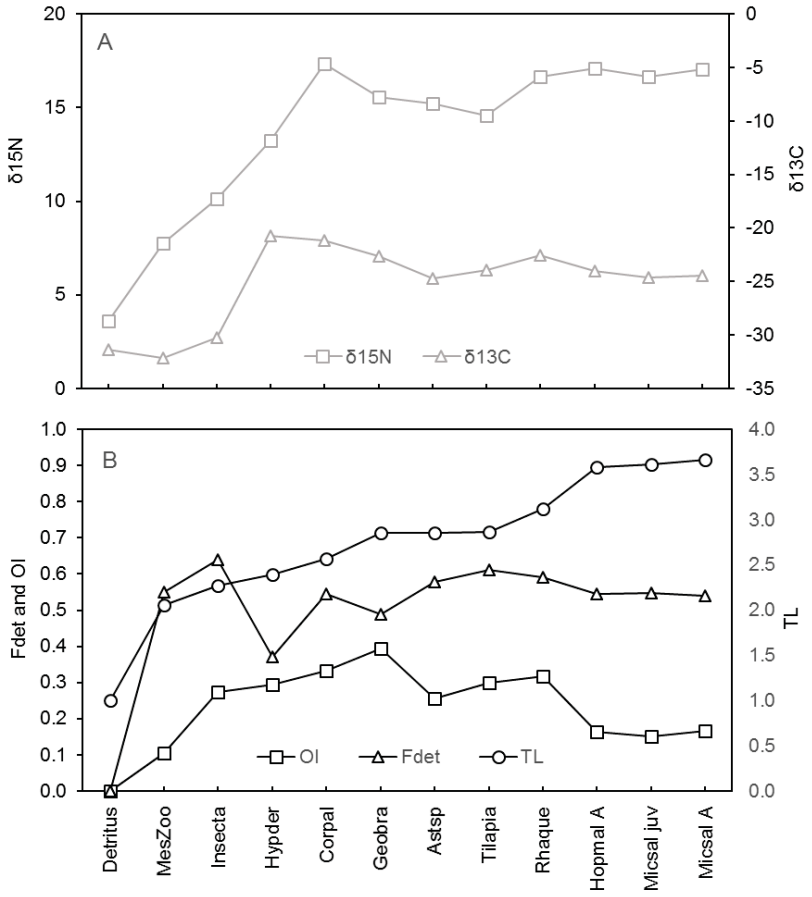

Figure 6. **A** Mean δ^{13}C and mean δ^{15}N values ordered by Trophic Level (TL) from minimum to maximum according to the modeled groups: Detritus, MesZoo (mesozooplankton, Cladocera and Copepoda), Insecta, Hypder (*Hypostomus derbyi*), Corpal (*Corydoras paleatus*), Geobra (*Geophagus brasiliensis*), Astsp (*Astyanax* spp.), tilapia, Rhaque (*Rhamdia quelen*), Hopmal A (*Hoplias malabaricus* adult), Micsal juv (*Micropterus salmoides* juvenile 1 and 2), and Micsal A (*Micropterus salmoides* adult). **B** Main axis represents Flow from detritus (Fdet) and Omnivory Index (OI), and secondary axis represents TL.

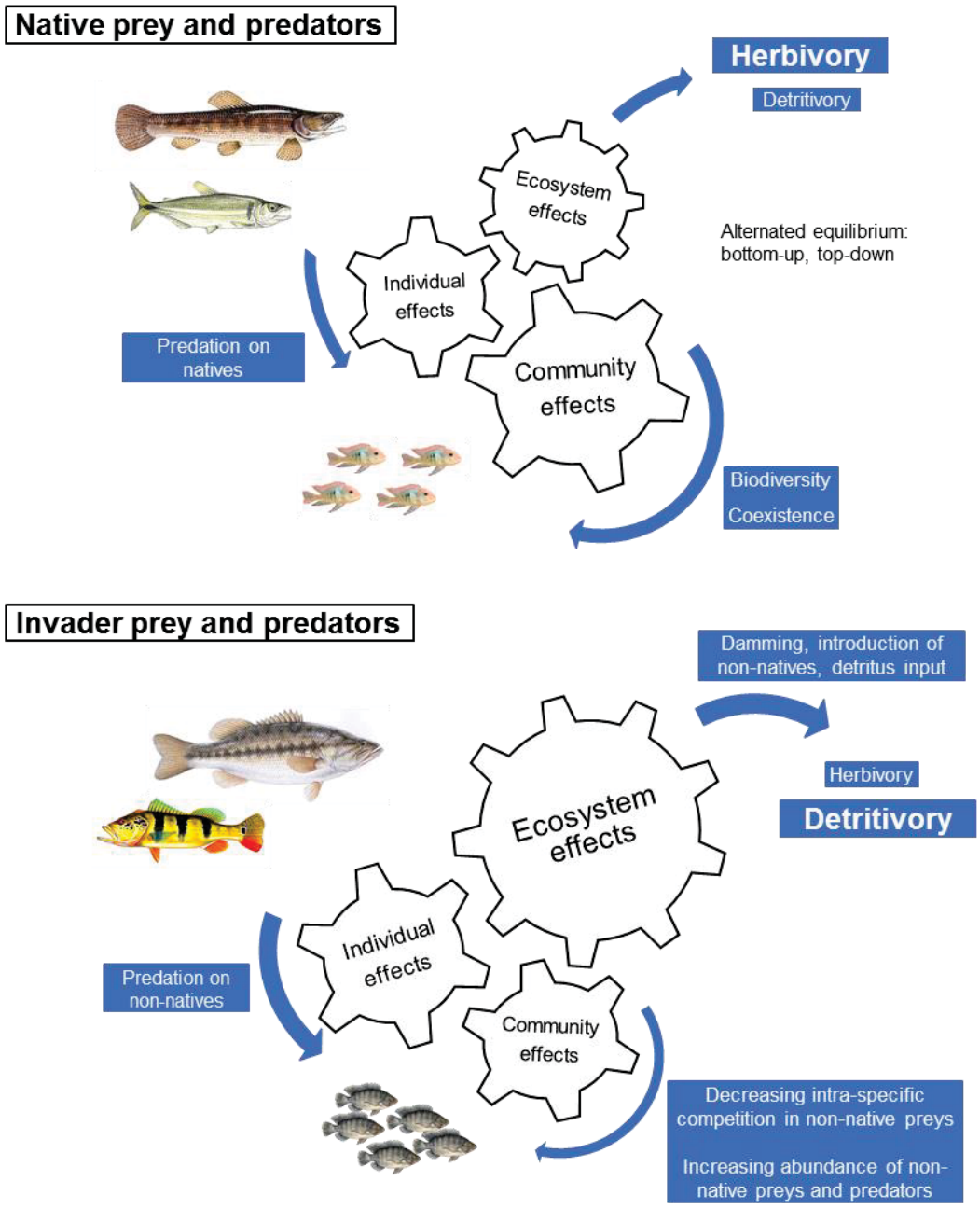

Figure 7. Snowball effects: In both scenarios (native/invader prey and predators), predation is largely dependent on detritus cycling (intermediate consumers feeding on benthos and detritus), but the influence of invaders is disproportional at the ecosystem level. Arrows and engines (in blue) indicate, respectively, the intensity of processes and effects size. Community effects could arise from interactions between individuals, without a noticeable impact on the ecosystem, for instance, predation avoidance by aggregation. Otherwise, an increase in the mean turbidity from this interaction could indicate an ecosystem effect.

Adults and J2, the classes represented in the stable isotope analysis, did not differ with respect to carbon sources (t = 0.81, df = 50.73, P = 0.42), but did differ with respect to nitrogen sources (t = 2.08, df = 52.76, P < 0.05, Figure SM6). Adults of *M. salmoides* had a greater range of δ^{15}N than juveniles, which was also reflected by TL.

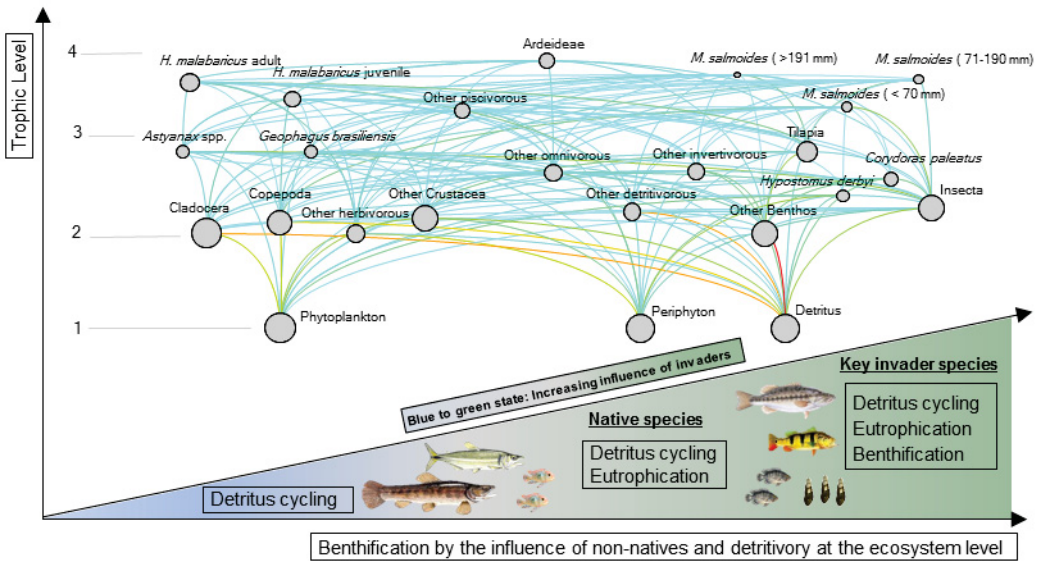

Figure 8. Blue to alternative green states towards "benthification" by the increasing influence of invaders and detritivory at the ecosystem level. Less representative groups: Other birds, Other Insectivorous, *Phalacrocorax brasilianus*, and *Rhamdia quelen* were omitted. Circles indicate biomasses, connect lines follows the diet matrix, and warming colors indicate interaction strengthening (Adapted from Bezerra et al. 2018).

Discussion

Our results suggest a generalized state of biotic homogenization in lentic fresh waters under the influence of damming and dominance of bottom-feeding species. The trophic downgrading is broadly described in terrestrial and aquatic environments (Estes et al. 2011), but the underlying mechanisms are obscure, and their link with invasional biology and secondary invasions was not observed until now. In line with the study case of the Passaúna reservoir, the low trophic level predominance of bottom-feeding in such "dam environments" Johnson et al.

(2008) worldwide shows that damming can be related to the occurrence of non-native, generalist prey and predators, which can trigger cascading effects towards benthic detrital pathways (see also Bezerra et al. 2018).

The prospected mechanisms of trophic homogenization described here (i.e., this dominance of bottom-feeding fish in low TL) can be attributed to the invader aspect of non-natives. Owing to its rapid somatic and population growth and significant resistance to environmental alteration (Canonico et al. 2005, Deines et al. 2016), non-native such as tilapia seems highly adaptable to the predation pressure (Bwanika et al. 2006) of *M. salmoides* and serves as the preferred food item in its diet. Indeed, tilapia foster detrital cycling by consuming mosquitoes (larval phase, probably their preferred prey in artificial reservoirs) and a variety of other detritivores, much more than other compartments (Starling et al. 2002). More than species, we must understand these invaders as functional groups. Then, benthification patterns could be expanded to the co-occurrence of tilapia (or another invader with bottom-feeding habits) and other non-native predators such as *Cichla monoculus* Agassiz, 1831 interacting with negative effects to native species, such as *Oligosarcus longirostris* Menezes & Géry, 1983 (Figure 7). It was observed in less diverse regions under drought effects, in which the available biomass of invaders in intermediate TL's was dominated by tilapia (Bezerra et al. 2018). Cascading effects should be expected with an increase in allochthone detritus and autochthone cycling by microorganisms and benthic invertebrates (Cole et al. 2006), the which could be attributed to the biomass production on benthos (Cremona et al. 2016).

Despite the stronger ecosystem impacts of *M. salmoides* adults, juveniles began feeding on large individuals of tilapia and other bottom-feeding species very early, relying heavily on tilapia (especially juvenile 2) as compared to other diet items, therefore triggering the cascading effects discussed here. Top-predators had massive nitrogen accumulation rates, and, consequently higher TL's than adults of other top predator native species, such as *H. malabaricus* and *R. quelen*. Beyond serving as prey, intermediate consumers such as tilapia and the native species *G. brasiliensis*, *H. derbyi,* and *C. paleatus* stimulate nitrogen cycling in the food web of reservoirs by the foraging on benthos (Lowe-McConnell 2000, Canonico et al. 2005, Bezerra et al. 2018). The eutrophication of freshwaters is related to the presence of tilapiines (Starling et al. 2002). The

increase in TL with increasing carbon sources, and alternatively, no variation on carbon sources due to increasing TL could highlight the restriction to the consumption of carbonated sources to low trophic levels. Their high $\delta^{13}C$ probably reflects heavy feeding upon CH4 rich or recycled heterogeneous food sources, such as microorganisms, the remains of animals, and plants (Fish and Carpenter 1982, Cremona et al. 2016). Carbon sources were only indirectly related to TL's and a better reflection of carbon sourcing (Post 2002).

Commonly, fish are limited by nitrogen in artificial environments (Cole et al. 2006, Holtgrieve et al. 2011), among other sources, because of the presence of N2-fixing cyanobacteria and other N-rich sources (Darchambeau et al. 2014), which can be related to the N-based fertilizers employed in aquaculture (Quesada et al. 2013) and to agricultural activities in surrounding areas (Stein and Klotz 2016). Indeed, recent studies emphasize the role of the bacterial loop as bottom-up support, instead of the phytoplankton by itself (Darchambeau et al. 2014). Considering the general human pressure on lakes and reservoirs, the deposition of reactive nitrogen could be the cause for nitrogen limitation (Holtgrieve et al. 2011). The level of detritivory could be another point related to the tilapia's effects. At the ecosystem level, it could result in eutrophication and a decrease in the weight at the capture of top-predator fish (Attayde et al. 2011).

Tilapia and carp are considered responsible for increasing detritivory rates associated with increasing habitat heterogeneity not only in reservoirs but in urban ecosystems in general (Ossola et al. 2016). The common carp (*C. carpio*) is a common invader included in "other omnivores" in our approach (see Material and methods). Members of this group are no less critical than tilapias as ecosystem engineers (Estes et al. 2011) and omnivore-planktivore species in shallow reservoirs worldwide (Liu et al. 2007, Matsuzaki et al. 2009, Colvin et al. 2015). An occasional spillover of these fish to downstream rivers added to eutrophication and ecosystem level effects (Blois et al. 2013, Pinnegar et al. 2014) to the role of *M. salmoides* as a keystone group at the community level. This is of concern since tilapiine cichlids, e.g., members of the genera *Coptodon*, *Oreochromis* and *Tilapia* are the most widespread group of non-native fishes worldwide (Canonico et al. 2005, Cassemiro et al. 2018), presently cultured in the immense majority of reservoirs in South America (Lima Junior et al. 2018). Such introductions were huge in Brazilian freshwaters since the 1970s (Ortega et al.

2015), and now achieved a critical stage in which they should be monitored in water quality assessments (Gondwe et al. 2011).

Given the spread of tilapia as the primary protein source in the fish aquaculture (Deines et al. 2016), the passion for *M. salmoides* and other bass fish in the sport fishery makes imminent their effects as co-occurring invaders in natural environments. Indeed, *M. salmoides* is a top-predator introduced in more than 50 countries for sports fishing (Jackson 2002, Froese and Pauly 2016), including Neotropical reservoirs (Britton and Orsi 2012). As a large and widespread fish, *M. salmoides* previously impacted the native community (Shelton et al. 2008). In most of places, *M. salmoides* reduced and/or extirpated the native fish fauna (Jackson 2002, Takamura 2007, Ellender et al. 2011, Natsumeda et al. 2015), exerting a stronger predation pressure than native predators (Alexander et al. 2014) or other non-natives (Trumpickas et al. 2011). Along with *M. salmoides*, adverse ecological effects due to the introduction of tilapiine fishes have been reported throughout the world (Deines et al. 2016). Without resource limitation, this is, in the presence of invaders such as tilapia, populations of *M. salmoides* could readily reach a density equilibrium and optimal growth rates, with juveniles and adults increasing in competitiveness with the native biota. In the food web of the Sítios Novos reservoir, Brazil, the consumption of apparently "*cul-de-sac*" species by tilapia is huge and results in positive feedback further benefiting tilapia and other invader predators and reinforcing dominance and determinism within the system (Bezerra et al. 2018). The dominance of "*cul-de-sac*" species, previously justified in the absence of predators (Twardochleb and Olden 2016), but now shown as a food source for invaders, could represent a benthification state.

Overall, biotic homogenization and eutrophication, related to widespread invaders, can be one of the immediate consequences of an invasional meltdown (Simberloff and Holle 1999, Britton and Orsi 2012, Hossain et al. 2013) in some reservoirs. Nevertheless, available evidence for the original Invasional Meltdown Hypothesis (IMH) covers a range of processes, communities, and ecosystems (Gurevitch 2006, Jeschke et al. 2012, Saul and Jeschke 2015). Positive feedbacks from interacting invaders are among recognized processes shaping the biodiversity, in the area ecology and conservation biology (Gurevitch 2006). Now, many studies focus on the facilitation at a community level, but few

evaluated feedback mechanisms with consequences to the ecosystem (Gurevitch 2006, Jeschke et al. 2012). We hope to have stimulated further investigations, particularly effects of the co-occurrence of damming, biological invasions, and benthification. Our results point only to one consequence of this obnoxious engagement, biotic homogenization, which is compromising ecosystem services and threatening the native fish fauna through, not only increase competition and predation (Weyl 2008, Sun et al. 2010, Sanches et al. 2012) but unpredictable ecosystem alterations.

We highlight that consequences of introductions and interactions among non-natives are dependent on scale and habitat, as well as on the recipient community and novel interactions with the non-native community. Undeniably, reservoirs can also add to the local economy. An impoundment increases the water surface area and reservoirs are whiling to the introduction of game fish and top-predators (Liew et al. 2018). New introductions in previously invaded systems can also alleviate the native community, such as suggested by antagonistic effects of introduced crayfish on invader bullfrogs, in China (Liu et al. 2018). However, the precautionary principle is a warranty on the secondary effects of new introductions. Then, we reinforce the utilization of this principle, before such enormous interventions on natural and artificial environments. The literature is vast, a recent review of the presence of native and non-native fish communities under anthropogenic impacts resulted in non-deterministic patterns in lentic and lotic artificial environments (Liew et al. 2018). An extensive review of threats to South American environments incorporates a more comprehensive collection of effects of non-native introductions, biological invasions, and related aspects (Bezerra et al., 2019).

Thus, we believe to have represented a tendency towards the dominance of bottom-feeding fish species related to damming, introductions, and trophic downgrading. Mechanisms behind the trophic homogenization can be referred to lentic systems under intense pressure for introductions and that sample most of their components locally. We controlled the stochasticity with Bayesian statistics in all the procedures employed (Mixed effect model in the analysis of meta-data, Ecoranger in the Ecopath, and SIAR in the Stable Isotopic modeling) and the resulting patterns of all three approaches were well correlated. Considering the introduction of tilapia and its predators, a future of non-native species driving

ecosystems is imminent in aquatic environments (Ossola et al. 2016) where the incoming economic problems are conspicuous. The feedback loop highlighted here could shape an acceleration of the effects by itself, at the ecosystem level, thereby becoming inexorable.

FINAL CONSIDERATIONS

In summary, this thesis reveals that riverine ecosystems (this is such as the Paraná river floodplain) can be enough complex to not be reduced to the determinism expected in recent hypotheses related to damming and introduction of non-natives, this is, benthification and oligotrophication of freshwater environments. Other processes related to biotic homogenization, trophic downgrading, and biological invasions are selecting mesopredators in low trophic levels, including pelagic species frequently associated with underwater structures (e.g., macrophytes and terrestrial plants). It was clear that the biotic homogenization was related to the domination of benthopelagic in low trophic levels. One could argue for the good conservation status of the floodplain given the increasing biomass of native groups. Otherwise, such success co-occurs with the success of non-native benthopelagic.

Alternatively, the benthification process is taking place on reservoirs around the world, and policymakers should be aware about it. At least in Brazil, the management of reservoirs does not account to the effect of biological components properly. Activities are concentred in the environment (phosphorus, nitrogen), or, scarcely, on basal components of the food web (phytoplankton). A plan to fill reservoirs should also include a plan to deal with detritus accumulation and cycling into the ecosystem. Also, the management of the biota colonizing these new environments, as well as their feedbacks with the environmental quality, which should account with the evolutive advantages of bottom-feeding species, particularly non-natives. It is essential to control the spread of omnivore and generalist non-natives, such as tilapia (*Oreochromis niloticus*), due to their propagule pressure, their influence on the environmental quality, and their advantages over the native biota.

Finally, with this thesis, we describe a multi-level process of biotic homogenization from populations to the ecosystem in a neotropical floodplain

and in reservoirs throughout the world. Even with the water regulation in the Paraná river floodplain by upstream reservoirs, flood pulsed had a crucial role in explaining the biomass functional groups from 2000 to 2017. We highlight the importance of this flood pulse in order to keep up with the community and ecosystem processes. Contrarily to natives, many non-natives does not answer to the flood pulse, therefore, floods can be a check point to the management of non-natives, when they are more vulnerable than natives.

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SUPPLEMENTARY MATERIAL

TABLES

Table SM1. Biomass, Size, and Density (BSD) trends (regression, student's *t* test) of Benpel - Benthopelagic, Dem - demersal, Pel – pelagic functional groups of fish. Estimated value (ß). Standard Error (SE). Statistical parameters representing the distribution of values are average (avg), inter-quartile range (IQR), maximum (max), median, standard deviation (sd), and variance (var).

Group		Net				Seine			
		ß	SE	*t*-value	*P*-value	ß	SE	*t*-value	*P*-value
Biomass									
Community	max	**0.039**	**0.017**	**2.294**	**0.025**	-0.049	0.036	-1.353	0.181
	median	**0.037**	**0.007**	**5.690**	**<0.001**	-0.023	0.016	-1.392	0.169
	avg	**0.022**	**0.007**	**3.229**	**0.002**	-0.012	0.015	-0.786	0.435
	IQR	-0.001	0.008	-0.067	0.947	-0.019	0.017	-1.148	0.255
	sd	**0.009**	**0.004**	**2.470**	**0.016**	-0.011	0.008	-1.316	0.193
	var	**0.038**	**0.015**	**2.468**	**0.016**	-0.040	0.034	-1.180	0.242
	RIQR	-0.228	0.311	-0.734	0.465	0.008	0.009	0.922	0.360
	Rsd	-0.185	0.218	-0.850	0.398	0.005	0.005	0.974	0.334
Native	max	**0.038**	**0.018**	**2.104**	**0.039**	-0.069	0.041	-1.667	0.100
	median	**0.041**	**0.009**	**4.721**	**<0.001**	-0.008	0.020	-0.416	0.679
	avg	**0.029**	**0.008**	**3.608**	**0.001**	0.005	0.018	0.261	0.795
	IQR	-0.008	0.009	-0.871	0.387	-0.010	0.023	-0.443	0.659
	sd	0.009	0.005	1.845	0.070	0.004	0.008	0.504	0.616
	var	0.040	0.020	1.939	0.057	0.018	0.037	0.488	0.628
	RIQR	0.049	0.526	0.093	0.926	-0.006	0.010	-0.576	0.567
	Rsd	-0.099	0.404	-0.245	0.807	-0.007	0.005	-1.261	0.212
Nonnative	max	**0.024**	**0.011**	**2.135**	**0.037**	-0.034	0.039	-0.867	0.389
	median	**0.034**	**0.009**	**3.801**	**<0.001**	**-0.052**	**0.021**	**-2.405**	**0.019**
	avg	**0.017**	**0.007**	**2.345**	**0.022**	-0.034	0.018	-1.912	0.060
	IQR	0.021	0.011	1.957	0.055	**-0.042**	**0.021**	**-2.030**	**0.047**
	sd	**0.011**	**0.004**	**2.825**	**0.006**	-0.017	0.010	-1.630	0.108
	var	**0.040**	**0.015**	**2.677**	**0.009**	-0.058	0.040	-1.461	0.149
	RIQR	**-0.110**	**0.043**	**-2.535**	**0.014**	**0.024**	**0.011**	**2.112**	**0.039**
	Rsd	**-0.072**	**0.030**	**-2.436**	**0.018**	0.014	0.007	1.871	0.066
Benpel	max	**0.070**	**0.020**	**3.611**	**0.001**	-0.070	0.038	-1.829	0.072
	median	**0.051**	**0.009**	**5.566**	**<0.001**	-0.019	0.016	-1.192	0.238
	avg	**0.034**	**0.009**	**3.917**	**<0.001**	-0.008	0.014	-0.538	0.593
	IQR	**0.030**	**0.010**	**3.085**	**0.003**	-0.006	0.019	-0.303	0.763
	sd	**0.018**	**0.005**	**3.977**	**<0.001**	-0.008	0.009	-0.952	0.345
	var	**0.072**	**0.019**	**3.813**	**<0.001**	-0.027	0.037	-0.734	0.466
	RIQR	2.406	5.016	0.480	0.633	0.002	0.009	0.182	0.856

	Rsd	1.880	3.886	0.484	0.630	0.003	0.005	0.559	0.578
Dem	max	0.019	0.015	1.278	0.206	-0.054	0.062	-0.871	0.387
	median	0.019	0.011	1.740	0.087	0.023	0.044	0.531	0.597
	avg	0.006	0.008	0.740	0.462	0.038	0.038	1.009	0.317
	IQR	-0.020	0.014	-1.422	0.160	**-0.102**	**0.040**	**-2.540**	**0.014**
	sd	0.001	0.006	0.107	0.915	**-0.053**	**0.026**	**-2.023**	**0.048**
	var	0.006	0.024	0.266	0.791	**-0.288**	**0.137**	**-2.094**	**0.041**
	RIQR	1.380	1.139	1.211	0.230	0.089	0.203	0.440	0.662
	Rsd	0.872	0.802	1.086	0.281	0.069	0.233	0.297	0.767
Pel	max	-0.025	0.020	-1.230	0.223	0.081	0.071	1.136	0.260
	median	0.009	0.015	0.603	0.549	-0.093	0.049	-1.910	0.061
	avg	-0.001	0.014	-0.066	0.948	-0.080	0.047	-1.689	0.097
	IQR	**-0.045**	**0.017**	**-2.586**	**0.012**	**0.089**	**0.033**	**2.660**	**0.010**
	sd	-0.016	0.010	-1.580	0.119	0.014	0.031	0.458	0.649
	var	-0.045	0.030	-1.497	0.139	-0.017	0.112	-0.153	0.879
	RIQR	**0.392**	**0.165**	**2.370**	**0.021**	0.077	0.051	1.504	0.138
	Rsd	**0.323**	**0.158**	**2.045**	**0.045**	**0.116**	**0.043**	**2.702**	**0.009**
TL2	max	**0.055**	**0.017**	**3.166**	**0.002**	-0.087	0.045	-1.937	0.057
	median	**0.081**	**0.007**	**11.238**	**<0.001**	-0.044	0.023	-1.962	0.054
	avg	**0.058**	**0.006**	**9.287**	**<0.001**	-0.012	0.019	-0.624	0.535
	IQR	-0.009	0.011	-0.850	0.399	-0.030	0.025	-1.222	0.226
	sd	0.006	0.005	1.154	0.253	0.008	0.012	0.639	0.525
	var	0.026	0.021	1.247	0.217	0.070	0.062	1.132	0.262
	RIQR	0.276	0.461	0.600	0.551	0.003	0.011	0.308	0.759
	Rsd	0.290	0.360	0.807	0.422	-0.006	0.006	-0.935	0.353
TL3	max	0.011	0.018	0.628	0.532	-0.021	0.038	-0.536	0.594
	median	0.008	0.010	0.785	0.435	-0.022	0.018	-1.225	0.225
	avg	-0.004	0.009	-0.420	0.676	-0.013	0.017	-0.737	0.464
	IQR	**0.022**	**0.010**	**2.157**	**0.035**	-0.017	0.020	-0.838	0.405
	sd	**0.011**	**0.005**	**2.317**	**0.024**	-0.008	0.009	-0.876	0.384
	var	**0.043**	**0.019**	**2.264**	**0.027**	-0.028	0.039	-0.722	0.473
	RIQR	-0.034	0.065	-0.518	0.606	0.010	0.010	1.037	0.304
	Rsd	-0.022	0.046	-0.478	0.634	0.005	0.006	0.996	0.323
Tl4	max	0.006	0.021	0.311	0.757	-0.041	0.042	-0.968	0.337
	median	-0.002	0.016	-0.147	0.884	-0.044	0.035	-1.260	0.213
	avg	-0.005	0.015	-0.345	0.731	-0.048	0.033	-1.450	0.153
	IQR	-0.011	0.010	-1.079	0.285	-0.007	0.027	-0.270	0.788
	sd	0.005	0.007	0.636	0.527	-0.016	0.020	-0.777	0.441
	var	0.017	0.022	0.759	0.451	-0.063	0.084	-0.746	0.460
	RIQR	0.149	0.489	0.305	0.762	0.097	0.233	0.418	0.678
	Rsd	0.072	0.362	0.198	0.844	0.115	0.251	0.460	0.648
Size									
Community	max	**0.018**	**0.010**	**1.915**	**0.060**	-0.022	0.035	-0.623	0.536
	median	**0.018**	**0.005**	**3.950**	**<0.001**	-0.007	0.012	-0.648	0.519
	avg	**0.016**	**0.004**	**4.032**	**<0.001**	0.001	0.014	0.011	0.991
	IQR	-0.005	0.005	-0.929	0.357	-0.010	0.022	-0.460	0.647
	sd	-0.001	0.002	-0.665	0.508	0.007	0.010	0.727	0.470
	var	-0.004	0.006	-0.631	0.530	0.037	0.039	0.946	0.348
	RIQR	-0.002	0.001	-1.871	0.066	8.597	15.131	0.568	0.572
	Rsd	**-0.001**	**0.001**	**-2.623**	**0.011**	6.301	12.388	0.509	0.613
Native	max	0.001	0.011	0.036	0.972	-0.058	0.039	-1.492	0.141
	median	**0.024**	**0.006**	**4.265**	**<0.001**	0.013	0.016	0.793	0.431
	avg	**0.018**	**0.004**	**4.217**	**<0.001**	0.019	0.016	1.185	0.240

	IQR	-0.002	0.006	-0.300	0.765	0.020	0.028	0.712	0.479
	sd	-0.003	0.002	-1.140	0.259	**0.025**	**0.011**	**2.203**	**0.031**
	var	-0.008	0.007	-1.102	0.275	**0.119**	**0.046**	**2.597**	**0.012**
	RIQR	-0.002	0.002	-1.160	0.250	-0.052	0.747	-0.070	0.945
	Rsd	**-0.002**	**0.001**	**-2.863**	**0.006**	0.128	0.718	0.179	0.859
Nonnative	max	0.038	0.017	2.170	0.034	-0.005	0.050	-0.103	0.918
	median	**0.024**	**0.006**	**3.636**	**0.001**	-0.021	0.014	-1.509	0.136
	avg	**0.018**	**0.006**	**3.107**	**0.003**	-0.024	0.018	-1.333	0.187
	IQR	-0.011	0.008	-1.245	0.217	-0.039	0.022	-1.764	0.082
	sd	-0.001	0.003	-0.200	0.842	-0.003	0.013	-0.214	0.831
	var	-0.002	0.010	-0.235	0.815	-0.005	0.047	-0.106	0.916
	RIQR	**-0.004**	**0.002**	**-2.163**	**0.034**	-0.181	0.330	-0.549	0.585
	Rsd	-0.001	0.001	-1.885	0.064	-0.257	0.407	-0.631	0.530
Benpel	max	**0.040**	**0.013**	**3.163**	**0.002**	-0.011	0.039	-0.291	0.772
	median	**0.022**	**0.005**	**4.069**	**<0.001**	0.007	0.011	0.603	0.549
	avg	**0.026**	**0.005**	**5.610**	**<0.001**	0.008	0.013	0.580	0.564
	IQR	-0.016	0.009	-1.764	0.083	-0.011	0.020	-0.540	0.591
	sd	0.001	0.003	-0.116	0.908	0.009	0.011	0.809	0.421
	var	0.001	0.009	-0.046	0.964	0.043	0.039	1.105	0.273
	RIQR	**-0.006**	**0.002**	**-2.839**	**0.006**	-0.629	0.410	-1.532	0.130
	Rsd	**-0.002**	**0.001**	**-2.863**	**0.006**	-0.364	0.385	-0.946	0.347
Dem	max	0.002	0.013	0.149	0.882	-0.018	0.062	-0.291	0.772
	median	**0.016**	**0.006**	**2.518**	**0.014**	0.053	0.048	1.115	0.269
	avg	0.001	0.006	0.019	0.985	0.062	0.038	1.617	0.111
	IQR	-0.007	0.008	-0.857	0.394	-0.076	0.039	-1.951	0.056
	sd	0.001	0.003	0.323	0.748	-0.024	0.028	-0.865	0.391
	var	0.002	0.008	0.237	0.813	-0.134	0.141	-0.946	0.348
	RIQR	-0.001	0.002	-0.683	0.497	0.127	0.187	0.681	0.499
	Rsd	0.001	0.001	0.316	0.753	0.183	0.209	0.873	0.386
Pel	max	**0.039**	**0.013**	**3.139**	**0.003**	-0.027	0.066	-0.414	0.680
	median	0.011	0.009	1.158	0.251	**-0.179**	**0.044**	**-4.081**	**<0.001**
	avg	0.011	0.009	1.284	0.204	**-0.157**	**0.043**	**-3.636**	**0.001**
	IQR	0.014	0.009	1.600	0.115	-0.016	0.024	-0.658	0.513
	sd	**0.015**	**0.007**	**2.199**	**0.032**	-0.041	0.028	-1.493	0.142
	var	0.025	0.014	1.773	0.081	-0.193	0.108	-1.784	0.081
	RIQR	0.002	0.002	1.089	0.280	-0.214	0.105	-2.037	0.046
	Rsd	0.002	0.002	1.478	0.144	**-0.580**	**0.232**	**-2.497**	**0.016**
TL2	max	0.002	0.013	0.124	0.901	-0.055	0.050	-1.095	0.278
	median	**0.038**	**0.006**	**6.643**	**<0.001**	0.008	0.022	0.370	0.712
	avg	**0.033**	**0.005**	**6.829**	**<0.001**	0.028	0.020	1.421	0.160
	IQR	**-0.023**	**0.008**	**-3.070**	**0.003**	**0.062**	**0.029**	**2.141**	**0.036**
	sd	**-0.011**	**0.003**	**-4.332**	**<0.001**	**0.059**	**0.013**	**4.581**	**<0.001**
	var	**-0.031**	**0.008**	**-4.166**	**<0.001**	**0.284**	**0.056**	**5.042**	**<0.001**
	RIQR	**-0.008**	**0.002**	**-4.670**	**<0.001**	-0.255	0.228	-1.119	0.267
	Rsd	**-0.005**	**0.001**	**-7.299**	**<0.001**	-0.223	0.208	-1.074	0.287
TL3	max	**0.063**	**0.015**	**4.334**	**<0.001**	-0.018	0.047	-0.380	0.705
	median	-0.003	0.005	-0.568	0.572	-0.006	0.011	-0.585	0.560
	avg	0.007	0.005	1.383	0.172	-0.016	0.015	-1.094	0.278
	IQR	0.012	0.010	1.209	0.231	**-0.063**	**0.023**	**-2.790**	**0.007**
	sd	**0.009**	**0.003**	**2.835**	**0.006**	-0.013	0.012	-1.008	0.317
	var	**0.026**	**0.009**	**2.768**	**0.007**	-0.035	0.044	-0.806	0.423
	RIQR	0.002	0.002	0.875	0.385	-0.846	1.265	-0.669	0.506
	Rsd	**0.002**	**0.001**	**2.003**	**0.049**	-0.370	1.092	-0.339	0.736

TI4	max	0.008	0.016	0.524	0.602	-0.051	0.048	-1.069	0.290
	median	0.001	0.008	0.133	0.894	**-0.124**	**0.041**	**-3.029**	**0.004**
	avg	-0.011	0.008	-1.452	0.151	**-0.092**	**0.039**	**-2.353**	**0.022**
	IQR	0.001	0.011	0.050	0.961	0.006	0.027	0.217	0.829
	sd	**0.011**	**0.005**	**2.263**	**0.027**	-0.010	0.022	-0.481	0.632
	var	**0.032**	**0.013**	**2.410**	**0.019**	-0.052	0.086	-0.605	0.548
	RIQR	0.001	0.002	0.454	0.651	0.037	0.018	1.990	0.052
	Rsd	**0.003**	**0.001**	**2.446**	**0.017**	0.037	0.021	1.752	0.086
Density									
Community	max	-0.001	0.016	-0.077	0.939	-0.069	0.037	-1.861	0.067
	median	**0.020**	**0.006**	**3.355**	**0.001**	-0.011	0.011	-1.049	0.298
	avg	**0.015**	**0.005**	**3.345**	**0.001**	-0.011	0.010	-1.176	0.244
	IQR	**0.025**	**0.007**	**3.442**	**0.001**	-0.028	0.014	-1.974	0.053
	sd	**0.008**	**0.003**	**3.128**	**0.003**	-0.011	0.007	-1.703	0.093
	var	**0.020**	**0.007**	**3.088**	**0.003**	-0.030	0.021	-1.456	0.150
	RIQR	**-0.005**	**0.002**	**-3.542**	**0.001**	0.008	0.005	1.716	0.091
	Rsd	**-0.002**	**0.001**	**-3.229**	**0.002**	0.004	0.003	1.314	0.194
Native	max	0.009	0.021	0.455	0.651	**-0.102**	**0.041**	**-2.519**	**0.014**
	median	**0.023**	**0.008**	**2.941**	**0.005**	-0.003	0.012	-0.284	0.777
	avg	**0.022**	**0.006**	**3.468**	**0.001**	-0.015	0.011	-1.344	0.184
	IQR	**0.022**	**0.007**	**3.412**	**0.001**	-0.031	0.017	-1.771	0.081
	sd	**0.012**	**0.004**	**3.285**	**0.002**	-0.009	0.007	-1.263	0.211
	var	**0.028**	**0.009**	**3.267**	**0.002**	-0.023	0.023	-0.996	0.323
	RIQR	**-0.005**	**0.001**	**-3.797**	**<0.001**	0.008	0.006	1.361	0.178
	Rsd	**-0.003**	**0.001**	**-3.370**	**0.001**	0.002	0.003	0.745	0.459
Nonnative	max	0.003	0.012	0.247	0.805	-0.032	0.039	-0.816	0.418
	median	0.003	0.008	0.425	0.672	-0.013	0.014	-0.952	0.345
	avg	0.002	0.005	0.465	0.643	-0.009	0.011	-0.813	0.419
	IQR	0.003	0.008	0.380	0.705	-0.023	0.016	-1.461	0.149
	sd	-0.001	0.003	-0.527	0.600	-0.008	0.007	-1.086	0.281
	var	-0.004	0.006	-0.583	0.562	-0.022	0.022	-0.983	0.329
	RIQR	-0.001	0.002	-0.427	0.670	0.007	0.005	1.560	0.124
	Rsd	0.001	0.001	0.302	0.763	0.003	0.003	1.038	0.303
Benpel	max	0.010	0.021	0.499	0.619	-0.072	0.037	-1.931	0.058
	median	**0.024**	**0.008**	**3.128**	**0.003**	-0.018	0.012	-1.560	0.124
	avg	**0.020**	**0.006**	**3.307**	**0.002**	-0.015	0.010	-1.440	0.155
	IQR	**0.031**	**0.007**	**4.085**	**<0.001**	**-0.033**	**0.015**	**-2.196**	**0.032**
	sd	**0.011**	**0.004**	**2.811**	**0.007**	-0.010	0.007	-1.487	0.142
	var	**0.026**	**0.009**	**2.782**	**0.007**	-0.026	0.023	-1.146	0.256
	RIQR	**-0.007**	**0.002**	**-4.177**	**<0.001**	0.009	0.005	1.773	0.081
	Rsd	**-0.003**	**0.001**	**-2.968**	**0.004**	0.003	0.003	1.105	0.273
Dem	max	0.014	0.013	1.108	0.272	-0.082	0.045	-1.817	0.074
	median	**0.015**	**0.007**	**2.130**	**0.037**	-0.016	0.021	-0.761	0.449
	avg	**0.009**	**0.004**	**2.043**	**0.045**	-0.021	0.018	-1.195	0.237
	IQR	0.011	0.010	1.116	0.269	-0.036	0.019	-1.938	0.057
	sd	0.005	0.003	1.753	0.084	-0.015	0.017	-0.880	0.383
	var	0.013	0.008	1.685	0.097	-0.038	0.041	-0.911	0.366
	RIQR	-0.003	0.002	-1.384	0.171	0.010	0.005	1.738	0.087
	Rsd	-0.001	0.001	-1.981	0.052	0.004	0.005	0.852	0.398
Pel	max	-0.002	0.022	-0.109	0.913	**0.194**	**0.040**	**4.817**	**<0.001**
	median	0.001	0.012	-0.022	0.983	**0.076**	**0.023**	**3.317**	**0.002**
	avg	0.001	0.008	0.010	0.992	**0.081**	**0.021**	**3.759**	**<0.001**
	IQR	-0.004	0.011	-0.325	0.747	**0.077**	**0.021**	**3.688**	**<0.001**

	sd	-0.002	0.005	-0.349	0.728	0.028	0.018	1.589	0.118
	var	-0.003	0.007	-0.452	0.653	0.047	0.053	0.881	0.382
	RIQR	0.001	0.002	0.295	0.769	**-0.026**	**0.007**	**-3.534**	**0.001**
	Rsd	0.001	0.001	0.311	0.756	-0.011	0.007	-1.706	0.094
TL2	max	-0.010	0.017	-0.573	0.568	**-0.167**	**0.039**	**-4.289**	**<0.001**
	median	**0.039**	**0.007**	**5.887**	**<0.001**	**-0.041**	**0.014**	**-2.900**	**0.005**
	avg	**0.029**	**0.004**	**6.769**	**<0.001**	**-0.041**	**0.012**	**-3.499**	**0.001**
	IQR	0.016	0.009	1.812	0.075	**-0.080**	**0.018**	**-4.410**	**<0.001**
	sd	**0.008**	**0.003**	**2.549**	**0.013**	**-0.020**	**0.009**	**-2.245**	**0.028**
	var	**0.019**	**0.008**	**2.474**	**0.016**	-0.049	0.031	-1.580	0.119
	RIQR	**-0.005**	**0.002**	**-2.857**	**0.006**	**0.028**	**0.006**	**4.467**	**<0.001**
	Rsd	**-0.003**	**0.001**	**-3.934**	**<0.001**	**0.010**	**0.004**	**2.486**	**0.016**
TL3	max	0.035	0.018	1.929	0.058	-0.027	0.038	-0.722	0.473
	median	0.006	0.007	0.792	0.431	0.003	0.013	0.242	0.809
	avg	0.003	0.006	0.603	0.549	0.005	0.011	0.442	0.660
	IQR	0.009	0.009	0.944	0.349	-0.011	0.017	-0.634	0.528
	sd	0.007	0.004	1.829	0.072	-0.006	0.008	-0.697	0.489
	var	0.017	0.009	1.796	0.077	-0.003	0.023	-0.120	0.905
	RIQR	-0.002	0.002	-0.908	0.368	0.001	0.005	0.179	0.858
	Rsd	-0.001	0.001	-1.574	0.120	0.001	0.003	-0.091	0.928
TL4	max	**0.050**	**0.025**	**2.019**	**0.048**	0.085	0.054	1.564	0.124
	median	0.013	0.011	1.130	0.263	0.046	0.024	1.900	0.063
	avg	**0.016**	**0.008**	**2.049**	**0.045**	0.045	0.022	2.001	0.051
	IQR	**0.019**	**0.009**	**2.116**	**0.038**	0.005	0.022	0.237	0.814
	sd	**0.013**	**0.005**	**2.401**	**0.019**	0.001	0.025	0.031	0.975
	var	**0.026**	**0.010**	**2.525**	**0.014**	-0.032	0.095	-0.331	0.742
	RIQR	**-0.004**	**0.002**	**-2.199**	**0.032**	-0.002	0.007	-0.256	0.799
	Rsd	**-0.003**	**0.001**	**-2.424**	**0.018**	-0.004	0.011	-0.414	0.681

Table SM2. Food web model of the Paraná river floodplain calibrated by the Trophic Level (TL). Functional Groups (FG) are a combination of trophic level, habit, size, and origin of fish species. See the Methods section of the main text for further details about the denomination of FG and the calculation of Biomass (B), Production to Biomass (PB), Consumption to Biomass (QB), Ecotrophic Efficiency (EE), and Production to Consumption (PQ).

	FG	TL	B	PB	QB	EE	PQ
1	4p5n	4.32	2.24	0.65	8.12	0	0.08
2	4p2.5n	4.31	1.71	0.8	9.31	0.33	0.09
3	4p2n	4.19	1.21	1	10.78	0.70	0.09
4	4p1.5n	4.17	1.07	1.82	12.75	0.64	0.14
5	4p1n	4.16	0.76	2.29	15.08	0.49	0.15
6	4p0.5n	4.04	4.13	4.72	29.21	0.37	0.16
7	4d5pn	4.73	5.81	0.47	1.13	0	0.42
8	4d5n	4.49	3.56	0.6	1.59	0.26	0.38
9	4d2.5n	4.34	3.11	1.21	2.20	0.68	0.55
10	4d2n	4.22	2.74	1.912	3	0.86	0.64
11	4d1.5n	4.19	1.77	1.29	3.92	0.43	0.33
12	4d1n	4.06	2.13	2.59	5.92	0.53	0.44
13	4d0.5n	4.04	2.09	7.51	15.88	0.51	0.47
14	4d5pnn	4.73	8.23	0.25	1.9	0	0.13
15	4d5nn	4.49	3.06	0.36	2.57	0.50	0.14

16	4d2.5nn	4.33	2.00	1.95	3.78	0.65	0.52
17	4d2nn	4.22	1.21	1.06	5.06	0.39	0.21
18	4d1.5nn	4.19	1.26	4.1	7.33	0.44	0.56
19	4d1nn	4.06	1.39	4.45	12.50	0.47	0.36
20	4d0.5nn	4.04	0.27	7.13	30.91	0.42	0.23
21	4bp1n	4.20	0.74	2.1	6.07	0	0.35
22	4bp0.5n	4.11	0.75	9.5	26.8	0.14	0.35
	4bpnn						
23	4bp2nn	4.28	6.88	1.8	2.59	0	0.7
24	4bp1.5nn	4.22	2.35	1.35	4.11	0.14	0.33
25	4bp1nn	4.20	1.35	1.98	6.46	0.17	0.31
26	4bp0.5nn	4.11	0.52	7.65	16.55	0.26	0.46
27	3p0.5n	3.5	0.01	9.5	47.5	0	0.2
28	3p1.5nn	3.78	2.75	1.97	9.87	0.22	0.20
29	3p1nn	3.63	1.55	2.67	16.97	0.37	0.16
30	3p0.5nn	3.50	1.53	8.5	43.86	0	0.19
31	3d1n	3.59	0.37	5.5	8.06	0.44	0.68
32	3d0.5n	3.3	6.55	11.5	25.93	0.10	0.44
33	3d1nn	3.59	0.53	3.323	5.75	0.51	0.58
34	3d0.5nn	3.3	0.49	9.9	19	0.78	0.52
35	3bp5pn	3.78	1.51	0.29	5.65	0	0.05
36	3bp5n	3.64	1.09	0.43	5.90	0.45	0.07
37	3bp2.5n	3.53	1.21	1.29	6.42	0.49	0.20
38	3bp2n	3.40	1.29	1.03	7.15	0.57	0.14
39	3bp1.5n	3.28	1.34	1.42	8.39	0.60	0.17
40	3bp1n	3.21	2.23	3.61	11.41	0.27	0.32
41	3bp0.5n	3.24	32.29	12.9	35.33	0.08	0.37
42	3bp5nn	3.64	4.33	0.85	3.56	0.06	0.24
43	3bp2.5nn	3.53	2.95	0.95	4.37	0.27	0.22
44	3bp2nn	3.40	1.69	1.23	5.50	0.37	0.22
45	3bp1.5nn	3.28	0.98	1.88	7.13	0.62	0.26
46	3bp1nn	3.21	0.81	4.82	9.86	0.56	0.49
47	3bp0.5nn	3.24	2.77	11.41	23.23	0.63	0.49
48	2p0.5n	2.7	0.01	20.15	75.7	0	0.27
49	2p0.5nn	2.7	0.14	10.5	90	0	0.12
50	2d5pn	2.97	1.52	0.3	2.19	0	0.14
51	2d5n	2.88	0.62	0.25	2.64	0	0.09
52	2d2n	2.79	1.06	1.65	3.68	0.14	0.45
53	2d1.5n	2.69	1.44	3.27	5.54	0.46	0.59
54	2d1n	2.61	9.33	7.86	10.93	0.06	0.72
55	2d0.5n	2.55	6.05	7.55	24.54	0.22	0.31
56	2d5pnn	2.97	2.55	0.7	2.89	0	0.24
57	2d5nn	2.88	1.15	0.8	3.39	0	0.24
58	2d2.5nn	2.72	2.07	1.06	4.08	0.11	0.26
59	2d2nn	2.74	1.09	1.24	5.27	0.18	0.24
60	2d1.5nn	2.66	0.83	2	7	0.69	0.29
61	2d1nn	2.59	0.72	6.17	9.93	0.32	0.62

62	2d0.5nn	2.55	12.50	14.34	29.65	0.06	0.48
63	2bp5n	2.93	1.91	0.7	2.35	0.32	0.30
64	2bp2.5n	2.69	1.51	0.95	3.04	0.22	0.31
65	2bp2n	2.60	1.55	1.91	4	0.11	0.48
66	2bp1.5n	2.51	0.95	2.18	5.09	0.56	0.43
67	2bp1n	2.41	5.09	5.18	8.50	0.15	0.61
68	2bp0.5n	2.35	14.65	13.95	27.4	0.05	0.51
69	2bp5nn	2.93	2.25	0.56	3.72	0.34	0.15
70	2bp2.5nn	2.69	1.84	0.86	4.48	0.20	0.19
71	2bp2nn	2.60	1.23	1.12	5.53	0.23	0.20
72	2bp1.5nn	2.51	1.10	1.61	7.31	0.44	0.22
73	2bp1nn	2.41	0.82	3.81	11.41	0.54	0.33
74	2bp0.5nn	2.35	1.05	9.86	28.13	0.56	0.35
75	Prey4p	3.04	8.9	47	85.45	0.42	0.55
76	Prey4d	3.04	6	42	84	0.41	0.5
77	Prey4bp	3.14	3	39	78	0.38	0.5
78	Prey3p	2.5	12	51	102	0.66	0.5
79	Prey3d	2.5	14	44	88	0.58	0.5
80	Prey3bp	2.4	30	69	125.45	0.66	0.55
81	Prey2p	2	22	56	112	0.84	0.5
82	Prey2d	2	22	72	144	0.90	0.5
83	Prey2bp	2	23	70	140	0.83	0.5
84	PP	1	85	240	0	0.24	
85	S.OM	1	7.94			0.69	
86	Detritus	1	75			0.81	

FIGURES

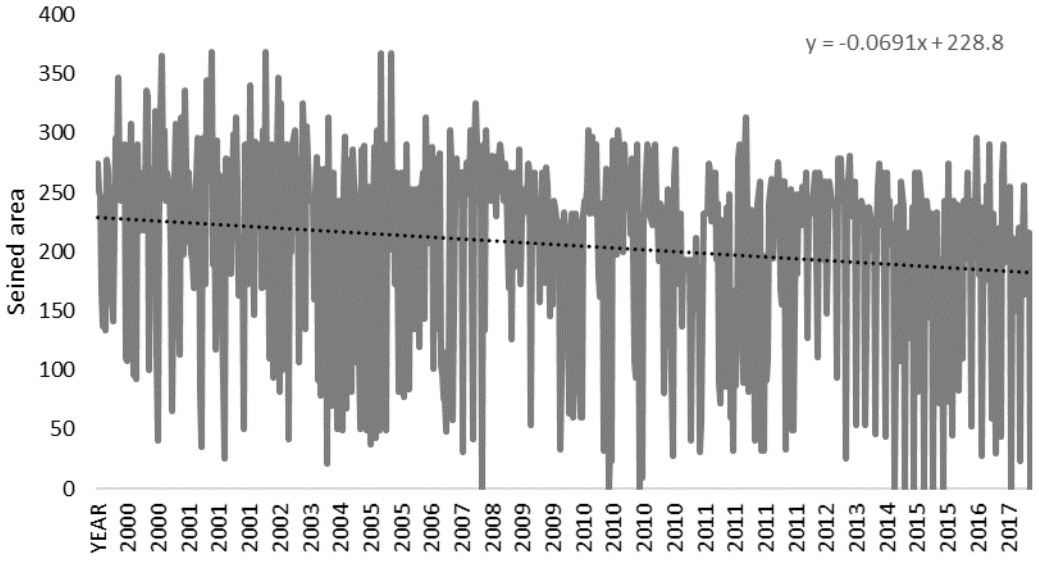

Figure SM1. Seined area used to the capture of fish species in the Paraná river floodplain, from 2000 to 2017.

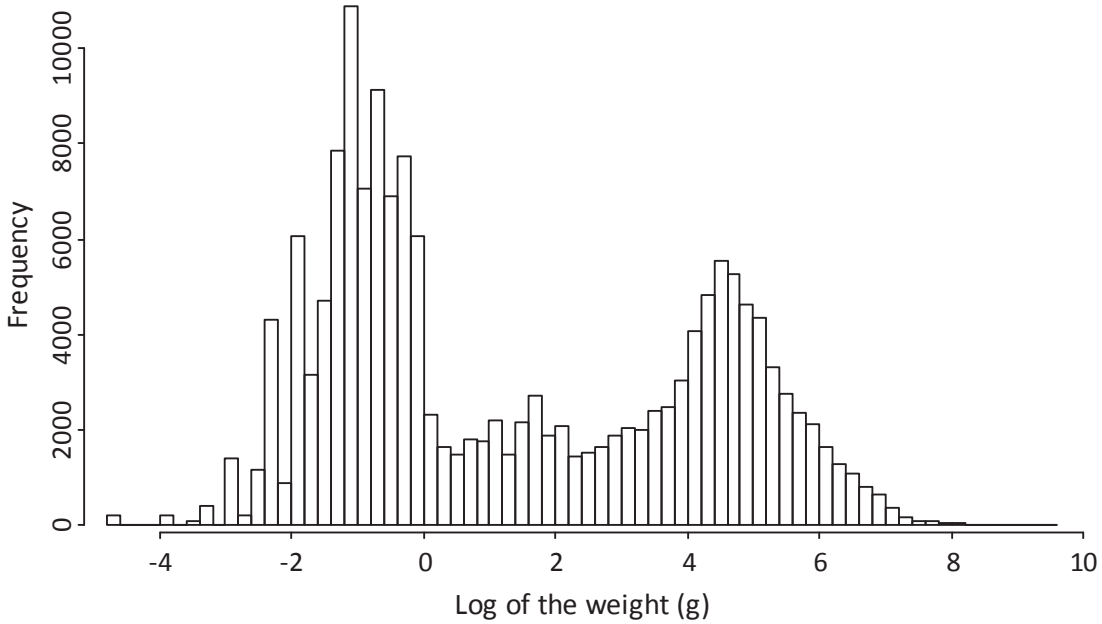

Figure SM2. Log-scale (g) distribution of weights of fish species captured in the Paraná river floodplain, from 2000 to 2017.

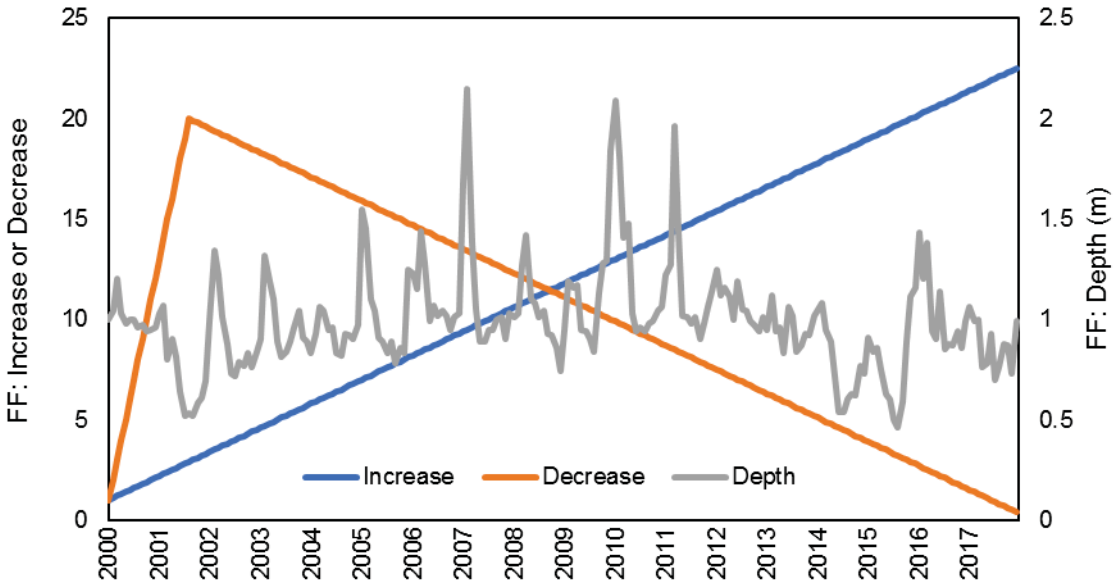

Figure SM3. Forcing Functions (FF) used to interpolate the biomass of functional groups in the food web model of the Paraná river floodplain, from 2000 to 2017. We retrieved the depth from the Paraná river station "Porto São José Jusante" (S22° 43' 03" W 53° 10' 48"). Data availability by the AGUASPARANÁ – Instituto de Águas do Paraná, at <aguasparana.pr.gov.br>, accessed in December 12, 2018.

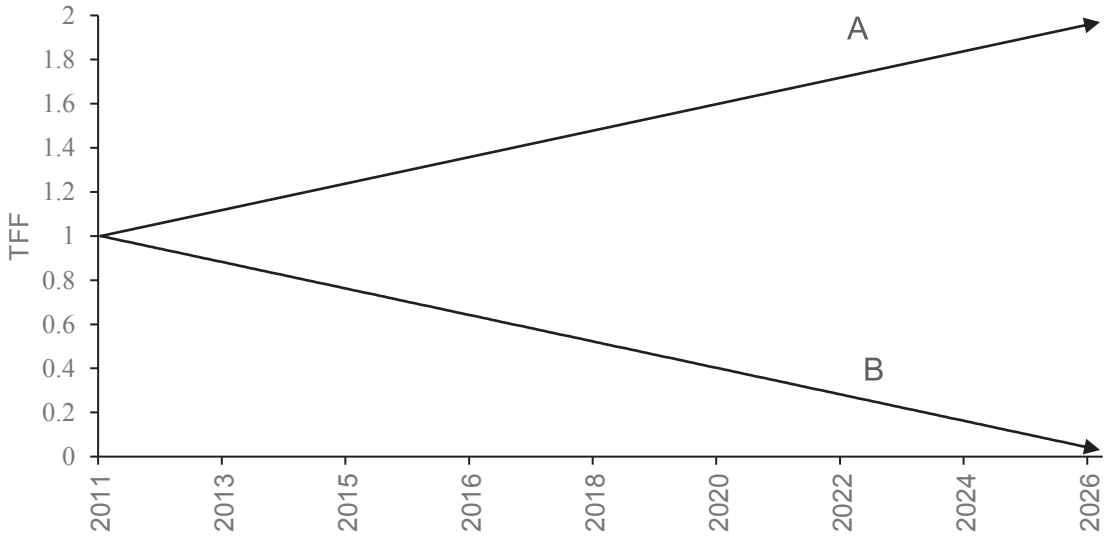

Figure SM4. Tilapia Forcing Function – TFF in two prospected scenarios of deterministic increasing (A) or decreasing (B) vulnerabilities, which could result from age and volume variation at a given reservoir. In general, reservoirs pass through three phases after the damming of the river: filling, a period of stabilization, and simulating equilibrium after 15 years, on average (Agostinho et al. 2016), that is the case of the Passaúna reservoir, built on 1985.

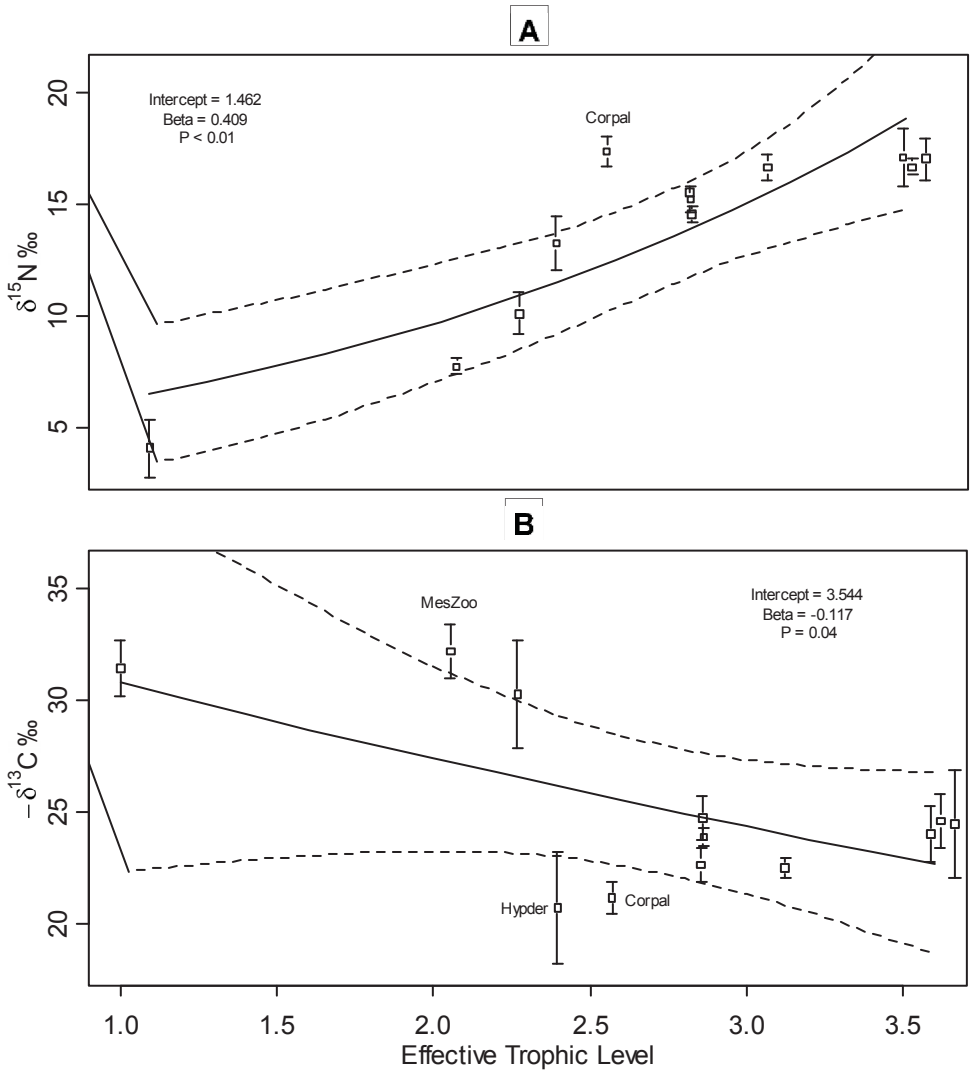

Figure SM5. General Linear Model Poisson-distributed (pGLM) of the mean δ15N values (A) according to the Effective Trophic Levels (ETL's), and quasi pGLM of the mean δ13C values in module (B). Solid lines are predicted values. Dashed lines are the interval among 5% and 95% of the predicted values. Outliers are identified: Corpal (Corydoras paleatus), Hypder (Hypostomus derbyi), MesZoo (mesozooplankton).

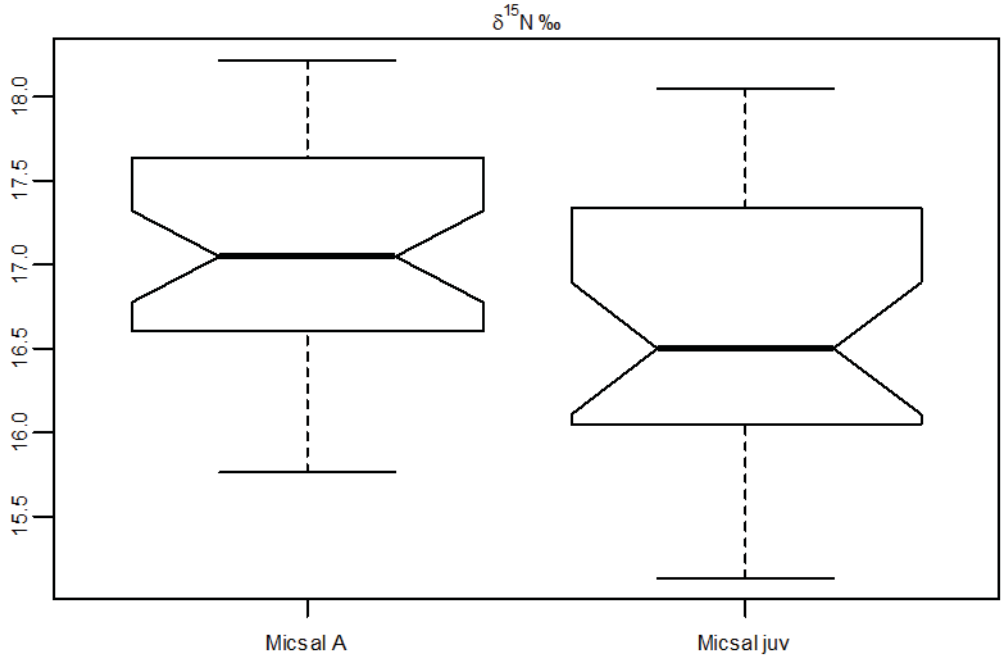

Figure SM6 δ15N-variation between keystone groups: Micsal juv (Micropterus salmoides juvenile 1 and 2) and Micsal A (adult; t = 2.08, df = 52.76, P < 0.05).